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BIOLOGY OF THE VERTEBRATES

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BIOLOGY

OF

THE VERTEBRATES

A COMPARATIVE STUDY OF MAN AND
HIS ANIMAL ALLIES

BY

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These pages, which he would have perused sympathetically, are dedicated to the memory of my father, who left me a teacher's torch to carry on.

PREFACE

The following pages are the outcome of over twenty years of teaching *Comparative Anatomy of Vertebrates* to premedical students and others. The "others" have crowded more and more into the picture, for while it is universally granted as essential that medical students should lay a firm biological foundation, it is not so generally realized that it may not be amiss for Everyman to gain some inside information about the "fearfully and wonderfully made" human mechanism, and how it came to be.

The book is divided into three parts.

Part One furnishes a necessary setting or introduction for the other two by emphasizing some of the outstanding features of various sister biological sciences most intimately related to Comparative Anatomy. They are Taxonomy, Chorology, Palæontology, Anthropology, Cytology, Histology, Embryology, and Pathology. The reason that Physiology is not specifically included in this review of cognate fields of study, is because it was found to be neither desirable nor possible satisfactorily to consider the function or physiology of the animal mechanism apart from its structure or anatomy. Hence the more general term of *Comparative Biology*, which includes somewhat more than the bare morphological aspect of the matter, appears upon the title page in preference to *Comparative Anatomy*, since it more nearly expresses the point of view employed.

In Part Two are grouped chapters dealing with the *mechanisms of metabolism and reproduction*, including the integument, systems of digestion, circulation, respiration, excretion, and reproduction, together with the glands of internal secretion.

Part Three is concerned with the *mechanisms of motion and sensation*, which may be regarded as particularly characterizing animal organisms.

It is expected that practical laboratory work upon various typical vertebrates will accompany the theoretical presentation of matter in the book. There has been no attempt to combine the two, since numerous excellent manuals and guides for dissection are now available. The author has found that the dogfish,

mud puppy, turtle, and white rat are the most useful and available forms to employ in these essential confirmatory exercises. At Brown University the students entering the course in Comparative Anatomy of the Vertebrates have already had a laboratory initiation with various invertebrates, the frog, and embryo pig.

There has been no determined attempt to avoid scientific names or technical terms in the text, whenever they are useful, and furthermore, that lazy man's device, a "glossary," as well as an extended bibliography of source materials, which would pad pages already corpulent, has purposely been omitted. A glossary has been omitted as it is assumed that the reader has access to a dictionary and is not indolent. As all technical terms are usually defined whenever first introduced, the index in most cases of doubt should satisfactorily guide the inquiring student to desired information. In the bibliography only a few outstanding books are mentioned and no attempt is made to cite the very many original papers involved. The student who has occasion to go back to such sources will find excellent lists in several of the books named, and will no doubt be advanced and resourceful enough to obtain whatever he wants without gratuitous assistance of this kind. The author confesses a fellow feeling in this matter of unasked for student aid for one Mr. George Baker, a contemporary of Shakespeare, who retained the ponderous Latin names of the herbs described in a foreign medical book which he translated into English, holding that it would do his readers good to look up the English equivalents, for, as he naïvely wrote in his preface: "I would not have every ignorant asse be made a chirurgeon by my booke." In any case it is the pursuit of knowledge rather than the final possession of it that is the chief delight of the scholar. If it were not for this fact there would be little excuse for, or satisfaction in attempting to make a book of this kind, which at best represents only a passing and incomplete picture of a changing body of knowledge.

The numerous illustrations, which the generosity of the publishers has made possible, have been gathered together from many sources. For the most part they have been redrawn or adapted from other pictures already published, in which case the source is indicated and for which grateful acknowledgment is hereby made. Many of the cuts from *The Human Skeleton* and *Genetics* by the author, as well as three figures from Hegner's *College Zoölogy*,

through the courtesy of The Macmillan Company, are used here again.

In preparing the pictures, aid was furnished by Miss Martha Whitmarsh, Miss Dorothy Walter, Mr. Harold Meyers, Mr. Joseph Kostecki, Professor J. Walter Wilson, and particularly by Miss Dorcas Hager. Professor Wilson has also critically read the entire manuscript, and Professor A. D. Mead some parts of it. The sympathetic insight and friendly suggestions of these two colleagues of many years has been a constant stimulus and support throughout the whole undertaking. Professor W. W. Swingle has cast a helpful eye over Chapter XVI. My niece, Miss Dorothy Walter, has given much expert assistance at all points in preparing the manuscript and reading the proofs, while the literary debt of long standing and increasing magnitude which I owe to my wife, Alice Hall Walter, is so great that there is no hope of ever discharging it.

If all the suggestions and criticisms from these various quarters, together with those of several other unnamed but appreciated contributing friends had been faithfully followed, this would no doubt be a better book. The responsibility for the volume as it stands, however, with its inevitable shortcomings, rests entirely upon my own shoulders.

To all the immediate helpers mentioned, as well as to the long line of biological workers, both obscure and famous, whose discoveries and ideas are our intellectual heritage today, I wish to acknowledge my great indebtedness. Last, but by no means least, I hereby express my sincere thanks to the stimulating young men and women, who for so many years have allowed themselves to be practiced upon in my classes.

H. E. W.

Brown University
November, 1927.

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BIOLOGY OF THE VERTEBRATES

PART ONE

THE BACKGROUND

CHAPTER I

INTRODUCTION

I. TYPE STUDY

No one knows how many different kinds of animals there are living today. When Aristotle (384–322, B.C.) wrote the first History of Animals he succeeded in rounding up only about 500 species, in spite of the fact that Alexander the Great, his famous pupil, gave special instructions to his conquering armies to aid in collecting from the ends of the earth the information about foreign animals which his old master so eagerly desired.

Since Aristotle's day explorers have stretched the horizon which then shut in the Mediterranean world, until now even Darkest Africa has been entirely crisscrossed, both poles have been trampled upon, and there is no considerable corner of the globe anywhere, on land or sea, from which authentic tales of animal life have not been brought back.

The authorities of the British Museum estimate that there are upwards of 600,000 species of living animals known to science, and in addition many more of extinct animals which have no living representatives and are known only by their fossil remains. The inquirer who would be informed about these things may well be appalled at the prospect of passing in review within a single lifetime of study this wealth of animal variety.

John Malpet, who in 1567 wrote one of the first "natural histories" in the English language, started his treatise with the hopeful sentence,—"Let us begin alphabetically with the adder." There is an easier way out of the situation, however, than by John Malpet's alphabetical method. Even Aristotle recognized in the make-up of animals a unity of plan which throws them into natural groups, so that when one knows about a single representative of a group he has considerable knowledge of all other kinds within that particular group.

Thus, familiarity with the mechanism and behavior of the house cat gives one a working knowledge of all other kinds of cats, such as the lion, tiger, lynx, leopard, ocelot, jaguar, wildcat, puma, cheetah, and panther. Much of the fascination that goes with the study of animal life lies in tracing resemblances and differences between various sorts of animals.

Although the number of kinds of animals is very great, the different general types or plans of structure are relatively few, so that the zoölogical student, by using the type-study method, may set out confidently and with a brave heart upon the ambitious quest of intellectually conquering all creation.

A list of the chief types of animals comprises:—PROTOZOA, CŒLENTERATA, ECHINODERMATA, PLATYHELMINTHES, ARTHROPODA, NEMATHELMINTHES, MOLLUSCA, ANNULATA, and CHORDATA.

II. COMPARATIVE STUDY

Of all animal types the chordate type is of most immediate interest, since it includes man. Many of the riddles connected with that much studied animal find their solution in the lower forms. For example, the parietal body, a conical projection about the size of a cherry stone buried between the lobes of the human brain, the use of which baffled anatomists for centuries, found a ready interpretation when Baldwin Spencer in 1886 dissected a New Zealand lizard, *Sphenodon*, by some called a "living fossil." He discovered that, in the chordate type, the "parietal body," or a part arising from it, probably is simply a degenerate eye, for, in this curious primitive animal, it reaches, with retina and nerve complete, all the way to a transparent window in the roof of the skull, and, in early life at least, may function as a third eye.

It is entirely true that frequently more may be learned of human development and structure by the intelligent examination of a dogfish, or some lower vertebrate, than by the study of the human body itself. This is due not so much to the greater availability of the lower animals for dissection and experimentation, as to the fact that parts of lower animals show stages through which the human body has passed in arriving at its present degree of complexity, and thus furnish the key for the interpretation of the why and wherefore of the "fearfully and wonderfully made" human mechanism. Herein lies the value of *comparative* biology.

The indirect path has thus often been the shortest way in the

history of science. For example, inquisitive Ben Franklin, out in the thunder-storm with his key and kite, made the first step towards harnessing electricity. The Frenchman, Daguerre (1789–1851), trying to discover some way to clean tarnished silver, blazed a path which has become a broad highway in photography and the colossal motion-picture industry, while Pasteur, a thinking chemist, interested primarily in the apparently remote subject of the shape of crystals, laid firm foundations for the far-reaching developments of bacteriology and modern medicine. When such facts as these are remembered, nothing about the structure or activities of any animal, however familiar or strange, becomes insignificant or trivial to the seeker after truth concerning man.

III. THE ESSENTIAL FEATURES OF EVERY ANIMAL TYPE

Every kind of living creature must possess machinery of some sort for accomplishing two fundamental things, namely, metabolism and reproduction. *Metabolism* includes all activities that concern the upkeep of the individual, such as the intake of energy by way of food, its release in the form of action which constitutes "living," and the disposal of waste products incident thereto. *Reproduction* provides for the continuation of the species upon the earth, often at the cost of the individual life. The former function may be designated as selfish and egoistic; the latter as unselfish and altruistic.

Fig. 1.—A typical insect, showing the *abdomen*, all-important as the chief region of metabolism and reproduction, the locomotor *thorax*, and the directive *head*.

A typical insect, for example, is made up of three easily distinguishable regions, in order of relative importance, the abdomen, thorax, and head (Fig. 1). In the large *abdomen* is lodged the principal machinery for metabolism and reproduction, that is, most of the digestive apparatus, the respiratory, excretory, and circulatory mechanisms, and the reproductive organs. The *thorax* is devoted primarily to locomotion, furnished as it is with three pairs of legs and usually two pairs of wings together with the muscles necessary to work

them, and is thus enabled to move the abdomen about to places where it can selfishly procure energy-producing food and unselfishly provide for the next generation. Finally, the *head*, with its battery of various sense organs and a correlating brain, is added, to direct the thorax where to go and what to do when it arrives, in the essential task of ministering to the abdomen. Many animals get along comfortably without head or locomotor device, but none can dispense with the all-important abdomen or something corresponding to it. Even in man that crowning glory, the head, of which he is apt to be especially proud, as well as the locomotor legs, become quite subsidiary when the body, which corresponds to the insect's abdomen, sends out the imperious call of hunger or of sex.

The function of metabolism is usually accomplished in a different way by animals than by plants, with the result that most plants remain stationary while most animals move about. The reason for this lies in the fact that green plants possess the power, in the presence of sunlight, of building up their foods out of universally distributed materials, such as carbon dioxide in the air, water, and various inorganic compounds in the soil. No animal can do this, so it comes about that all animals must find their energy, either directly or indirectly, in the stored supply already captured from the sun by green plants. This is why most animals are fated, like the Wandering Jew, forever to be travelers, a condition which necessitates in animal types some adequate device for locomotion and consequently an accompanying sensory equipment. The fact that certain animals, like oysters and corals, are sedentary, is the exception. "Their strength is to sit still" (Isaiah). In the case of these animals the dependence upon green plants, however, is quite as complete as among locomotor forms. They feed upon the microscopic plants that form the floating meadows of the ocean, and, therefore, have developed secondary devices for bringing this floating food to them.

IV. SYMMETRY

There are no animals with less than three dimensions, although some of the lower forms are so small as to necessitate very delicate instruments to determine their length, breadth and thickness.

The science of the form and shape of organisms is called *Morphology*. It is closely related to *Solid Geometry* with the difference

that the mathematician has little occasion to inquire, for instance, why one figure is a cube and another a sphere, while the biologist is constantly being challenged to explain the reason for the shape of each organism which he encounters in relation to its adaptation to the particular life that it leads. Moreover, the forms and figures that the geometrician deals with are the arbitrarily created children of the human mind without any modifying past, while the forms of animals and plants which the biologist considers are the products of an actual historical procession of ancestral shapes that have all left their determining impress.

Three fundamental shapes or forms among animals are recognized, and, as a result, three general types of symmetry, namely, spherical, radial, and bilateral. Each of these types may be camouflaged in various ways by secondary modifying qualifications. *Spherical symmetry* is rare. It is found only among microscopic animals, such as, the "sun animalcules," or Heliozoa of the protozoan type, which float, surrounded by water on all sides and without contact with anything solid. Many water animals, on the contrary, become attached, during a part of their life at least, and lead a sedentary plantlike existence. Such anchored animals are usually headless, and frequently develop a crown of radiating arms or tentacles, which enable them to reach out in every direction to explore as far as possible their neighborhood. This headless plan is the *radial type of symmetry*, which, in general, is characteristic of trees and stationary plants, of attached animals, and of some other aquatic animals whose food is brought to them floating in water. On land, where food does not float in a transporting medium, animals have to travel to obtain food when they are hungry, and this has made necessary the development of a directive head. A head end appears in many water animals, such as fishes, for example, but it is an absolute necessity for locomotor land animals. Whenever an animal moves persistently in one direction with reference to its own body, in other words whenever there is a head end established, there results *bilateral symmetry*. The body presenting this type of symmetry may be divided into halves only by means of the three planes which can be arranged with reference to length, breadth, and thickness. In radial symmetry, on the other hand, the number of divisional planes is practically indefinite, like the number of ways in which a sphere may be cut into similar halves or hemispheres.

The three planes (Fig. 2), bisecting length, breadth, and thickness, divide any head-ended animal into definite regions, very useful as landmarks in description, as follows:—

SAGITTAL PLANE dividing the body into RIGHT and LEFT HALVES;
TRANSVERSE PLANE dividing the body into ANTERIOR and POSTERIOR HALVES;
FRONTAL PLANE dividing the body into DORSAL and VENTRAL HALVES.

The sagittal and frontal planes are so named because of certain sutures in the human skull with which they coincide. It is obvious

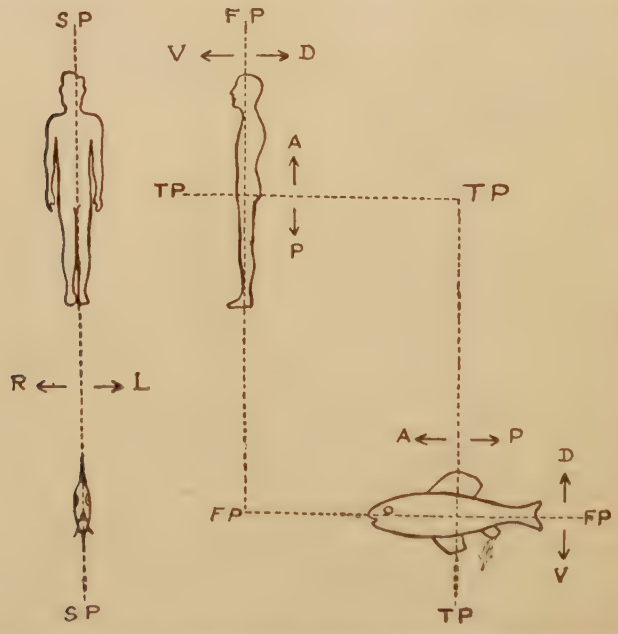


FIG. 2.—The planes of symmetry in bilaterally symmetrical animals, with the resulting regions. *S.P*, sagittal plane; *F.P*, frontal plane; *T.P*, transverse plane; *R*, right; *L*, left; *D*, dorsal; *V*, ventral; *A*, anterior; *P*, posterior.

that man moves with the *ventral* body-half in front, instead of the *anterior* body-half, because he is a head-ended, bilaterally symmetrical animal tipped up on end.

V. VERTEBRATE CHARACTERISTICS

In the vertebrate or craniate type (see page 15) there are certain distinguishing features that serve to mark off this type from all others. Of these the most diagnostic are the following:

1. A Living Endoskeleton

The skeleton, primarily a dorsal axis or vertebral column to which other parts are attached, is inside the body. It is made up of living tissues that continue to grow and so to meet the demands for an adequate scaffolding in a body of increasing size. This is why it is possible for vertebrates to become the largest known animals. Among non-vertebrates, such as molluscs and arthropods, the skeleton is outside the body, forming an imprisoning armor. Since it is a secreted structure, and consequently dead, it does not conveniently allow for extended growth, so that no one ever heard of a clam, a lobster, or an insect as large as an elephant, a whale, or a dinosaur.

2. A Notochord

Not every vertebrate has a backbone, made up of separate parts as the name "vertebrate" would indicate, but all possess, at least early in life, a dorsal axis of peculiar structure, called the *notochord*. A few primitive vertebrates retain the notochord throughout life but in most cases it is a transient, skeletal axis, which later is replaced by the backbone.

3. A Single, Tubular, Dorsal Nerve Cord

The central nervous system extends along the dorsal side of vertebrates in the form of a single tube, a result brought about by the manner of its development. This tube has a hollow enlargement at the end, called the brain. In very primitive animals, which have not yet acquired a definite nervous system, such as *Hydra* and other cœlenterates, the outside of the body serves the purpose of sensory mediator. Any structure as delicate and specialized as the nervous system, however, cannot become efficient as long as it remains on the outside. Hence, in all animals except the simplest, the nervous system becomes protectively buried within the body. In vertebrates the burial is by the process of *invagination*, that is, the outer layer of the body along the dorsal side grows so rapidly that a groove is formed, the walls of which

push down into the underlying tissues and finally close over to become a tube. Eventually this tube is entirely detached from the outer layer and buried beneath it. The successive stages in the formation of the vertebrate nerve cords are shown diagrammatically below in cross section (Fig. 3, A).

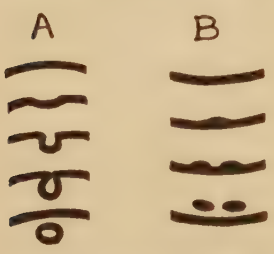


FIG. 3.—Successive stages in the migration of outside tissues to the inside. *A*, by invagination; *B*, by delamination.

In a typical invertebrate, such as a worm or an insect, the central nervous system is buried by a different manner of growth, called *delamination*. Here there is a thickening along the *ventral* side of the animal which eventually splits off inside, forming a solid, instead of a tubular nerve cord (Fig. 3, B). Frequently the delaminated nerve cord of invertebrates is double rather than single as in vertebrates.

4. A Postanal Tail

A true tail may be defined as a continuation of the vertebral column posterior to the anal exit of the food tube. That part of a lobster, for example, which is sometimes erroneously called the "tail," is not a true tail at all, but is really the *abdomen*, since the anus opens at the end of it. Each vertebrate has a true tail, ancestrally, embryonically, or throughout life. Even apparently tailless man in his early stages has a well-defined tail (Fig. 4), and there are numerous cases reported in medical literature of evident human tails that persist beyond embryonic life.

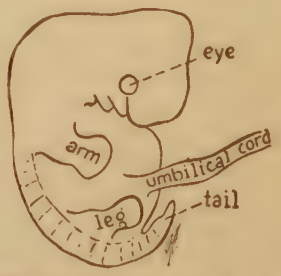


FIG. 4.—Lateral view of a young human embryo showing tail. (After Ecker.)

5. Never More than Two Pairs of Paired Appendages

Myriapods, or "thousand-legged worms," do not have as many legs as their name implies, but they have a large number. Other bilaterally symmetrical animals, such as marine worms and crustaceans, have a varying number of paired legs, while spiders and their allies have four pairs, and insects three pairs, usually

with additional wings, but vertebrates alone are limited to two pairs. This is a reasonable and logical number because four legs furnish the most efficient and economical support for any sort of an elongated bilaterally symmetrical object, such as a table top, a bedstead, or a horse. Certain vertebrates, it is true, have lost one or the other of their pairs of appendages, and snakes, for example, have lost both pairs. The only vertebrates with more than two pairs exist in the imagination of those artists of the olden days who painted a pair of gratuitous wings on the shoulders of their canvas angels.

6. Mouth Closed by a Lower Jaw

The anterior opening of the food tube is closed in various ways. In *Hydra* and many other primitive forms without jaws, the mouth is simply a puckerable hole. When jaws are present they may be arranged in a circle, as in some sea urchins, closing the mouth centripetally, or they may be side by side, closing the mouth laterally, as in arthropods, or finally, there may be a movable lower jaw, closing the mouth by lifting up, as among the vertebrates.

7. Pharyngeal Breathing Device

In fishes there are several porthole-like passages, or gill slits, penetrating through the walls of the food tube on either side of its anterior end. Within these gill slits hang feathery tufts of capillaries (gills), which rob the circulating water of its contained air and so accomplish "breathing." Gill slits, or traces of them, are present, at least in early life, in all vertebrates whether dwelling in water or out of it, even in reptiles, birds, and mammals, which never breathe by means of gills at any time during their life. Whenever breathing is accomplished by lungs, such organs develop as side alleys from this same anterior pharyngeal region of the food tube where the gills occur. No invertebrate breathes in this way, and, although many kinds of animals employ gills of various sorts, *pharyngeal gills* and *gill slits*, or traces of them, are peculiar to vertebrates.

8. Ventral Heart

The heart, which is the headquarters of the circulatory system, is ventrally located in vertebrates. In other animals when a heart is present, it is on the dorsal side.

9. Closed Blood System

In vertebrates the blood courses through a continuous system of tubes, known as arteries, veins, and capillaries. Invertebrates, on the contrary, at least certain ones, have an open blood system, that is, one in which the blood may pass freely back and forth between the proper blood vessels and surrounding spaces or sinuses. The contrast is remotely like that between the water-works of a modern city with water confined to pipes and mains, and the open ponds and streams of the country-side.

10. Hepatic Portal System

In vertebrates the food-laden blood always passes through a strainer-like capillary network (liver) before it arrives at the heart to be sent over the hungry body. Although other animals have organs that are called "livers" by courtesy, only vertebrates have a true liver, or clearing house where the blood is reorganized by addition and subtraction of various substances before being distributed to different parts of the body.

11. Red Blood Corpuscles

The red coloring matter in blood (hæmoglobin) is a complicated chemical substance, having the power of picking up and throwing

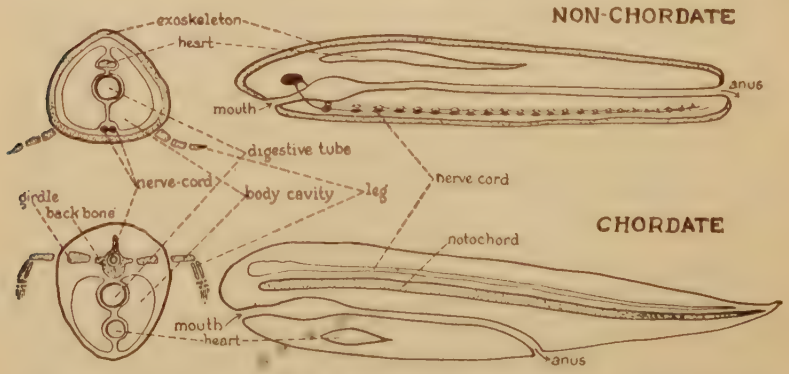


FIG. 5.—Comparative diagrams of the fundamental plans of a non-chordate (above) and a chordate (below).

off oxygen in the vital process of releasing energy. Among vertebrates hæmoglobin is lodged in special cells, the red blood cells, or "corpuscles." Whenever it is present in invertebrate

blood, it is dissolved in the plasma, or liquid part of the blood, since there are no red blood cells in invertebrates.

VI. COMPARATIVE DIAGRAMS OF CHORDATES AND NON-CHORDATES

A visualized summary of certain of the points of contrast between a generalized chordate and a corresponding non-chordate, is presented in Fig. 5.

CHAPTER II

KINDS OF VERTEBRATES (TAXONOMY)

I. TAXONOMY

It is quite necessary for the intellectual peace of mind of the student to arrange the different animals that he considers in some sort of a logical classification. This is *Taxonomy*.

Any good classification is much more than a simple convenience, since it expresses a compact summary of our knowledge of the origin and derivation of different animals. Consequently, to make any sensible classification it is necessary to know details of structure, internal and external, and something of the historical vicissitudes through which animals have passed.

In putting together animals of a kind the ideal criterion to employ is *relationship* rather than outward resemblance, and it is the particular province of comparative biology to discover relationships. Thus, a whale is properly classified with the mammals rather than with the fishes which it superficially resembles and with which it associates, because its common origin with mammals is indicated by the fact that, along with many other mammalian peculiarities, its young are born alive and are fed at first upon milk.

Owing to the incompleteness of our present knowledge about the blood-relationship of animals, there is still much controversy among taxonomists as to "who's who" in classification, but there is substantial agreement in the use of the following successive groups in which

like INDIVIDUALS make up SPECIES;
" SPECIES " " GENERA;
" GENERA " " FAMILIES;
" FAMILIES " " ORDERS;
" ORDERS " " CLASSES;
" CLASSES " " PHYLA;
" PHYLA " " KINGDOMS.

The manner of employing these groups may be illustrated by classifying a particular individual house cat, named "Tom" (Fig. 6). It will be seen that this particular cat finds himself successively in more and more inclusive groups, of less and less kinship, until finally, as a member of the vast animal kingdom, he has quite lost his identity. If now we go backward on the diagram

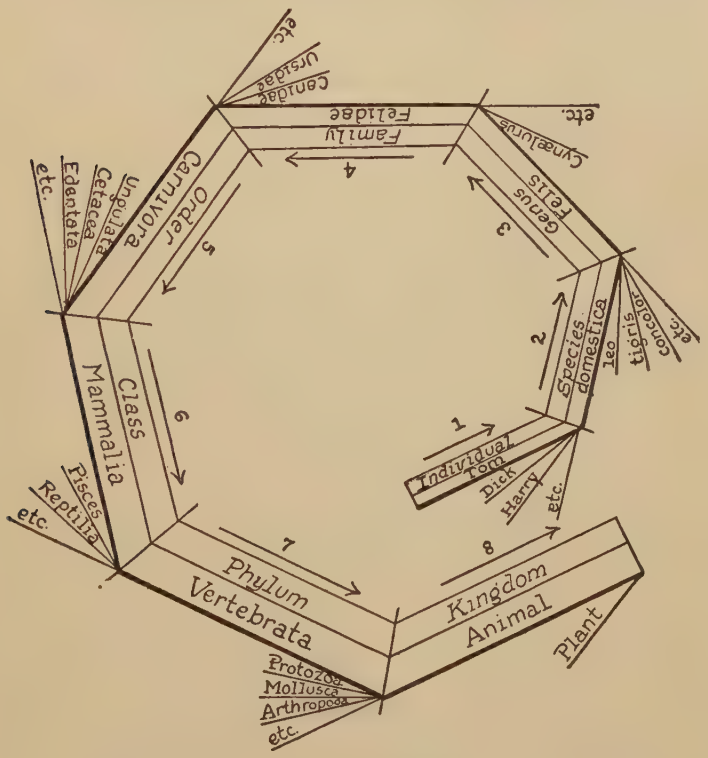


Fig. 6.—The taxonomy of a cat named "Tom."

from the animal kingdom end we find the individuality of "Tom" gradually emerging, until it may be finally concluded that he possesses at least not only all the characteristics of vertebrates listed in the preceding chapter, but that he has also all the structural apparatus necessary to make him a *carnivorous mammal*, that he resembles more or less intimately his distant cousins, the lions, tigers and their kind, and that he is very much indeed like other domestic cats.

II. SCIENTIFIC NAMES

It is necessary in the serious study of animals to employ scientific names. Common names like nicknames or pet names, may have only a local application and do not always lead to sufficient accuracy of determination. The Swedish naturalist Linné (1707–1777) introduced into biology a complete system of scientific naming. He employed Latin mostly in making up these names. This was advisable since Latin is a "dead" language, no longer subjected to the changes in form to which any spoken language is liable, and comes nearest to being the universal language of educated peoples of all tongues. He faithfully christened all the animals and plants known to science in his day with a scientific name, and even included himself, so that he is generally known by the Latin name of *Linnæus*.

A complete scientific name consists of three parts, that is, the name of the *genus* to which the animal belongs, the name of the *species*, and the name of the *namer*, or godfather, who does the christening. Thus, *Felis domestica*, *Linn.* is the proper scientific name for every common house cat, because these cats belong to the genus *Felis*, and to the species *domestica*, and were so named in the first place by *Linnæus* himself.

When the same kind of an animal is given two or more scientific names independently, as frequently occurs, the confusion is remedied by adopting the first name assigned, if it can be so determined. This is in accordance with the "law of priority."

In any scientific name the genus is invariably written with a capital letter and the species with a small letter, although it is permissible sometimes, when the species is named in honor of a person or place, to employ a capital letter for its name. In common practice the name of the namer, which is principally useful in determining priority in doubtful cases, is frequently omitted.

Every student of biology who sets out in earnest to excel, must conquer any childish aversion he may have for the imaginary terrors of scientific names and should acquire, as soon as possible, facility in the use of these important tools of his trade.

III. A ROLL CALL OF VERTEBRATE CLASSES

Before proceeding further with the consideration of the comparative biology of vertebrates it is necessary to pass in brief review the different vertebrates between which comparisons are to be made.

The phylum Chordata may be lined up in the following array:—

Subphylum I. PROTOCHORDA
Class 1. Hemichorda
Order 1. Enteropneusta
Class 2. Urochorda
Class 3. Cephalochorda
Subphylum II. VERTEBRATA
Class 1. Cyclostomata
Class 2. Pisces
Class 3. Amphibia
Class 4. Reptilia
Class 5. Aves
Class 6. Mammalia

1. Border-line Chordates

The important peculiarities which characterize the subphylum *Vertebrata* of the phylum *Chordata* have already been indicated in the first chapter. There are certain animals, however, which have difficulties in qualifying completely in all particulars as vertebrates, but are, nevertheless, classified as chordates. These interesting connecting links with the invertebrates may be called "border-line chordates," or *Protochordates*. They are subdivided into *Hemichorda*, *Urochorda*, and *Cephalochorda*.

A. HEMICHORDA

Balanoglossus auranticus, *Girard* (Fig. 7), may be taken as a representative of the Hemichorda, of which there are only a few genera. This small, fragile, worm-like animal has no common name, since it is not commonly known, an additional reason for resorting to the use of a scientific name. It possesses a rare interest for the comparative biologist since, unlike any true worm, it has a series of pharyngeal gill slits, a stiffening skeletal structure in the anterior region suggesting a notochord, three pairs of cœlomic pouches, and a nervous system consisting of dorsal and ventral strands extending lengthwise the body. The dorsal nerve strand, which is the larger, separates from the outside, in its anterior region at least, and is buried by invagination in true

FIG. 7.—*Balanoglossus*, a border-line chordate with gill slits. (After Bateson.)

vertebrate fashion. In most particulars *Balanoglossus* is wormlike in structural details, but the few vertebrate features just mentioned suffice to indicate its problematical position between vertebrates and invertebrates. It lives in mud at various localities along the Atlantic seashore where at low tide its burrows may be identified by peculiar coiled piles of castings (Fig. 8), much like those deposited by earthworms upon the land.

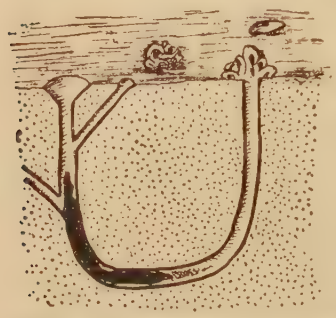


FIG. 8.—*Balanoglossus* in its tube 30-60 cm. deep in sand. (From Hesse, after Stiasny.)

Different species of the subphylum Enteropneusta are found widespread in similar habitats the world over. For example, Dr. W. E. Ritter, an authority upon this group of animals, discovered in 1896 during the Harriman Expedition, among other kinds along the shores of Alaska, a new genus, probably the most primitive of them all, which he christened *Harrimania* (Fig. 9), in honor of the expedition.

FIG. 9.—*Harrimania kupfferi, Ritter.* (After Spengel.)

B. UROCHORDA

The Urochorda are the marine *tunicates* or *ascidians*, so-called from a peculiar, baglike outer envelope or "tunic" with two openings, and also because their general appearance suggests an "ascidium," the Latin name for a primitive wine sac made of goatskin.

These degenerate representatives of the vertebrate idea are all marine organisms, living for the most part a colonial, sedentary life. *Molgula manhattensis, DeKay*, a common "sea squirt" found along the Atlantic shore attached to piles, floating seaweeds, and other objects, may be taken as a typical species. The essential features of its structure may be learned from the diagram of a simple ascidian (Fig. 10). It will be seen that water, containing oxygen and microscopic food particles, when taken in through the incurrent opening, may stream out through the large perforated pharynx (gill slits) into the surrounding chamber and so accomplish breathing, or the food particles in the

water may escape past the pharyngeal openings of the gill slits and reach the gullet, where they are then forwarded into the digestive tube itself. This is quite like the pharyngeal arrangement in fishes for breathing and feeding. The principal part of the mechanism which insures the transfer of food particles past the numerous gill slits to the gullet of a tunicate, is a ciliated groove, the *endostyle*, extending down the side of the pharynx. Sticky mucus is produced by the glandular walls of this groove and the cilia in the bottom of the groove create a current which causes the food particles to become entangled in the mucus. Thus a continuous rope of food-laden mucus is forwarded into the gullet. Moreover, the heart of the sea squirt is *ventral* in location, and the central nervous system, although reduced and insignificant in these sedentary animals, is *dorsal* and *hollow*, both typical features of vertebrates.

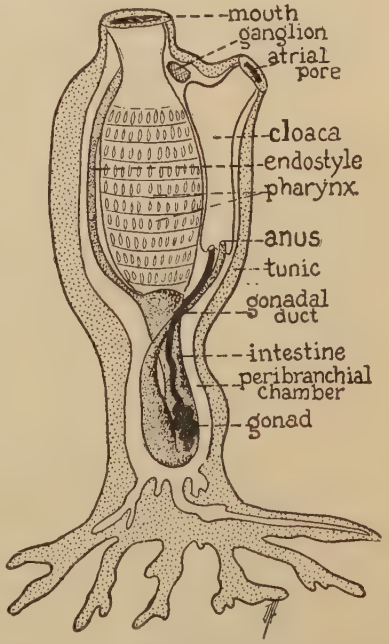


FIG. 10.—Organization of a simple tunicate. (After Haller.)

It is the early life of the tunicate, however, that gives the real key to its unmistakable relationship to true vertebrates which it so little resembles when superficially examined. The egg develops into a free swimming larva like a tadpole (Fig. 11), which shows in its locomotor tail an unmistakable notochord, and a single, tubular, dorsal nerve cord. This is the reason for the name of the group "Urochorda" (*uro*, tail; *chorda*, notochord). After the larva swims about for a while and grows somewhat in size it settles down on a suitable support and enters on its lifetime of stationary existence. The tail, no longer needed for locomotion, is transformed into other tissues and the tunicate thus sacrifices most of its birthright of vertebrate characteristics, that is, notochord and tubular dorsal nerve cord, for the doubtful advantages of sedentary serenity.

Some tunicates are colonial in habit and live connected together in more or less dependence upon each other, a state of affairs not uncommon among the lower animals, but which does not occur

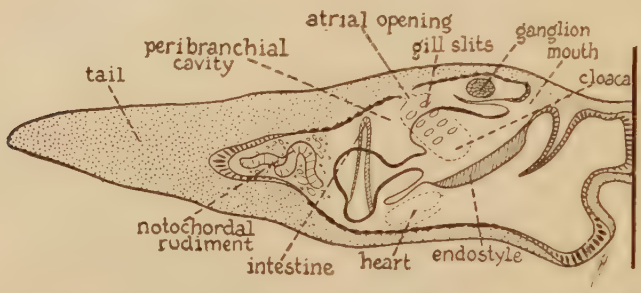


FIG. 11.—Diagram of a larval tunicate, *Clavelina*, just become attached. (After Seeliger.)

elsewhere among vertebrates. This compound or colonial manner of life is shown, for example, by *Botryllus* (Fig. 12), a small tunicate that grows in starlike, slippery patches over the surface of seaweeds that float in the shallow waters of the seashore. Here the in-

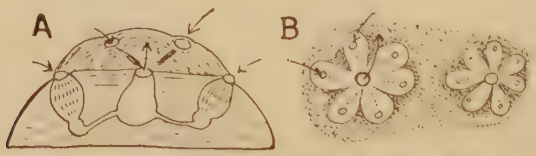


FIG. 12. *Botryllus*, a compound tunicate. *A*, section of a colony, showing the common exit; *B*, surface view of two colonies surrounded by a gelatinous mass, growing upon the flat surface of a bit of seaweed.

current openings of the different individuals are separate, being arranged in a circle around a common excurrent opening.

Other colonial tunicates, the beautiful transparent "chain Salpas," for example, are pelagic in habit, forming elongated rafts, which float near the surface of the ocean, usually many miles from land. Most primitive of all these humble cousins of the vertebrates are the microscopic *Appendicularia*, tiny ghostly creatures of the vast oceans which live a life of freedom and do not relapse, like other tunicates, into unambitious sedentary degeneration.

2. Cephalochorda

Of the chordate vertebrates, that have either a notochord or a backbone in adult life, the class *Cephalochorda*, so named

because the animals comprised in it have a notochord extending into the head, includes only two genera, *Branchiostoma* (usually known as *Amphioxus*) and *Asymmetron*, and less than a dozen species. These animals, because of the absence of a cranium or brain case, are sometimes called *Acraniata*. If they had a cranium they would have nothing to put into it, for they are brainless little creatures whose nerve cord fails to enlarge at its anterior end into anything like a brain, yet amphioxus has had enough written about it by scientists to fill more than one ponderous tome. The reason for this unusual distinction lies in the fact that it is the *simplest known vertebrate animal*, and contains the beginnings of many great things.

"It's a long, long way from Amphioxus
But we came from there!"

The unique biological significance of this elementary ancestor was first made known by Johannes Müller (1801–1858) almost a century ago, and now no book upon the higher animals is complete that does not reckon with this famous, tiny creature, in which the chordate plan is reduced to its lowest terms.

Amphioxus, or the "lancelet" as it is sometimes called, is an elongated, semi-transparent, fishlike animal of perhaps two or three inches in length when full grown, somewhat pointed at either end, as the Greek name (*amphi*, both; *oxus*, sharp) would indicate. In habit it is largely sedentary, lying buried in the sandy bottoms with its anterior end projecting, although some of the species of the genus *Branchiostoma* are pelagic. The lancelets dwell in tropical or semi-tropical seas in localities as far apart as the Bay of Naples, the coast of Peru, Japan, the Indian Ocean, California, the Philippines, West Indies, Australia, North Carolina, Hawaii, the Maldive Islands, and China. This wide distribution suggests the great antiquity of the type which, in spite of its poor means of locomotion, has had time to spread to the uttermost corners of the earth. Off the coast of Southern China, north of the Island of Amoy, amphioxus is so abundant that it forms an important food-fishery which has been worked by the Chinese for centuries. Professor S. F. Light, of the University of Amoy, writes:[1] "Here on this little strip of coast about 400 fishermen, using 200 small boats, are engaged for from two to four hours on the ebb tide of every calm day during the nine months from August to April of each

[1] *Science*, July 27, 1923.

year in dredging for amphioxus for the market. The catch averages about 2,600 pounds, well over a ton for each calm day during

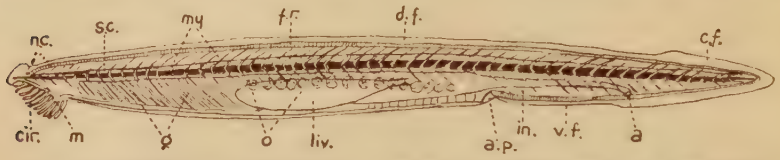


FIG. 13.—Diagram of amphioxus. *a*, anus; *a.p*, atrial pore; *c.f*, caudal fin; *cir*, cirri around mouth; *d.f*, dorsal fin; *f.r*, fin rays; *g*, gill slits; *in*, intestine; *liv*, liver; *m*, mouth; *my*, myotomes; *n.c*, notochord; *o*, ovaries; *s.c*, spinal cord; *v.f*, ventral fin. (After Perrier.)

the nine months of the fishing season and a total of hundreds of tons of amphioxus taken during the year!"

However, it is not as a source of Chinese food that the chief interest in amphioxus lies, but because in its development and structure it points the way in which the complicated conditions found in higher vertebrates take their rise. It will be necessary later on, when tracing the origin of various vertebrate organs, to refer repeatedly as a starting-point to the stage of development presented by amphioxus. Now brief attention is called to only a few of the more conspicuous peculiarities of this chordate "Adam and Eve."

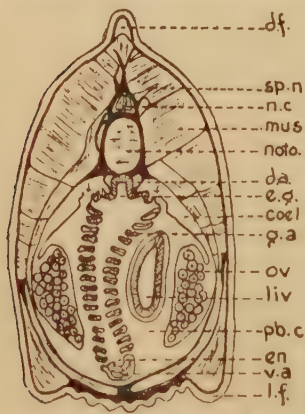


FIG. 14.—Cross section of amphioxus. *d.f*, dorsal fin; *sp.n*, spinal nerve; *n.c*, nerve cord; *mus*, muscle; *noto*, notochord; *d.a*, dorsal aorta; *e.g*, epibranchial groove; *cœl*, cœlome; *g.a*, gill arch; *ov*, ovary; *liv*, liver; *pb.c*, peribranchial cavity; *en*, endostyle; *v.a*, ventral artery; *l.f*, lateral fin. (After R. Hertwig.)

Reference to diagrams (Figures 13 and 14) will show the presence of (1) a typical *notochord*, extending the entire length of the body; (2) an *invaginated nerve cord* lying above it; (3) a *postanal tail*, and (4) an extended series of lateral *pharyngeal gill slits*. These gill slits are enclosed within a pharyngeal chamber which opens to the outside through a ventral "atrial pore," corresponding to the excurrent opening from the tunic cavity of the tunicates (Fig. 10). Along the floor of the pharyngeal chamber there extends an endostyle similar in structure and function to the endostyle of

tunicates. At the anterior end is a circle of bristle-like "cirri" that guard the mouth, and help to direct the microscopic food into it, while running along the dorsal side of the body and around the tail ventrally, is a continuous median fin. This fold of the skin, as it passes around the tail end, expands to form the conspicuous

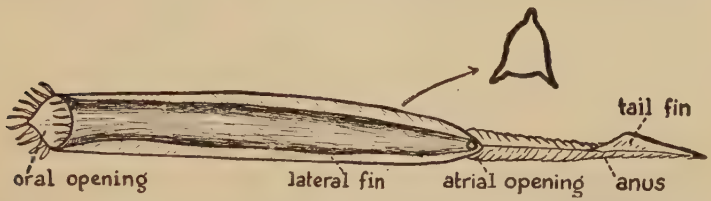


FIG. 15.—Ventral view of amphioxus, showing lateral fin folds, which are forerunners of the paired appendages of higher animals. (After Kirkaldy.)

"caudal fin," and when the fold reaches the region of the atrial pore anterior to the anal opening, it divides like a letter Y, and extends forward as lateral folds (Fig. 15). It is out of persisting parts of similar lateral folds, which are laid down temporarily in the embryos of higher vertebrates, that the paired locomotor appendages are formed (Fig. 16). The food tube is short, direct, and uncomplicated, and has growing out from it a blind sac, the *liver*, lined with glandular epithelium and supplied with a network of blood vessels that represents the beginnings of a vertebrate *hepatic portal system*, because the blood from the food tube has to pass this capillary strainer in the liver before it goes forward to the gills and thence over the body. There is no conspicuous heart present but a ventral blood vessel, lying below the pharynx is larger than the other blood vessels and is prophetic of a future vertebrate ventral heart in the higher forms.

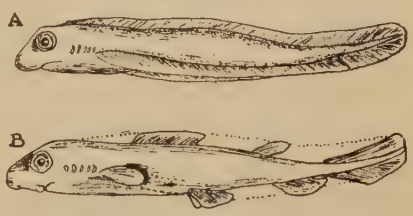


FIG. 16.—Diagram of the phylogenetic development of unpaired and paired fins. *A*, Amphioxus stage, with continuous fins; *B*, differentiated stage, with fins remaining after partial absorption of the primitive continuous fins. (After Wiedersheim.)

Unlike the tunicates or Urochordates, Cephalochordates as well as Hemichordates probably represent simple, primitive,

advancing animals, and not forms whose simplicity is the result of degradation.

3. Craniates

A. Cyclostomes

The lamprey eels (Fig. 17), and hagfishes, which show a great advance in the vertebrate series over the forms thus far considered are so different from other fishes that they have been placed in a class by themselves. They are called "cyclostomes" (*cyclo*, round; *stome*, mouth) for the reason that, instead of typical vertebrate jaws, they have round, jawless, sucker-like mouths by which they attach themselves to the sides of fishes or to other objects. When a hagfish thus fastens to a fish it may rasp a hole, with the filelike horny teeth attached to its muscular tongue, quite through the sides of its unfortunate host, and so eventually cause its death.

The cyclostomes are distinguished chiefly by the absence of certain customary fishlike structures. They are not only jawless

Fig. 17.—Lamprey eel, *Petromyzon*. (After Goode and Bean.)

but are also without paired fins, scales, swim bladder, cloaca, oviducts, true teeth, vertebræ, ribs, or bones of any kind. All are eel-like in shape, but are not to be confused with true eels, which have a bony skeleton including jaws, instead of a skeleton consisting only of a persistent notochord.

The larval lamprey has an endostyle and obtains its food by ciliary ingestion like amphioxus. During metamorphosis into the adult the endostyle becomes the thyreoid gland, to which further reference will be made in a later chapter.

Only a few genera are reported as belonging to North America. The best known are the hagfishes, *Myxine* (Atlantic) and *Polistotrema* (Pacific); the lampreys, *Petromyzon*, found both in fresh and salt water, *Ichthyomyzon* of the Great Lakes and Mississippi Valley, and the brook lamprey, *Lampetra*.

The hagfishes are particularly slippery creatures, producing often so much mucus, when uncomfortably confined in a bucket of water, that they thicken the water into a gluey mass. Linnæus describes *Myxine glutinosa* of Europe in compact Latin with the words: "*Intrat et devorat pisces; aquam in gluten mutat.*" Lampreys are used for food, particularly in Europe. Cicero bewailed the tendency of the young spendthrift Romans of his day because they spent altogether too much time in reveling at night and in feasting upon such delicacies as lampreys.

B. Fishes

Over one half of all the kinds of vertebrates are fishes. They form the dominant inhabitants of the waters of the earth which stretch out over considerably more area than the land masses. When Pliny (23–79 A.D.) wrote his *Historia Naturalis* he enumerated 94 kinds of fishes then known to the Roman world. Linnæus in 1735 listed 478. Jordan and Everman, in "Fishes of North America" (1886), describe 3112 American species, while the ichthyologists of the British Museum name about 20,000 species the world over at the present time. Approximately eight out of every twelve of these species are pelagic inhabitants of the open oceans, three are either coastal in distribution or found in inland waters, and one is a dweller down in the darkness of the deep sea.

Fishes vary enormously in size, all the way from the dainty *Mistichthys luzonensis, L.*, of the Philippines, which is only about half an inch long when full grown, to the colossal shark, *Rhinodon typicum, S.*, which, according to Hæmpel, has been known to attain a length of sixty-five feet. There is likewise a remarkable range in the body form of fishes, as indicated by representatives shown in outline in Fig. 18, A–G.

The key for understanding the fish plan is to be sought in the adaptation of these animals to life in water. For example, the generous tail, which frequently is more extensive than all the rest of the body, is a locomotor organ entirely effective in sculling through the resistant medium of water, but which would be quite useless out in thin air.

An elementary working assortment of fishes into their principal distinctive groups, is made up of five classes: Elasmobranchii, Holocephali, Ganoidei, Dipnoi, and Teleostei.

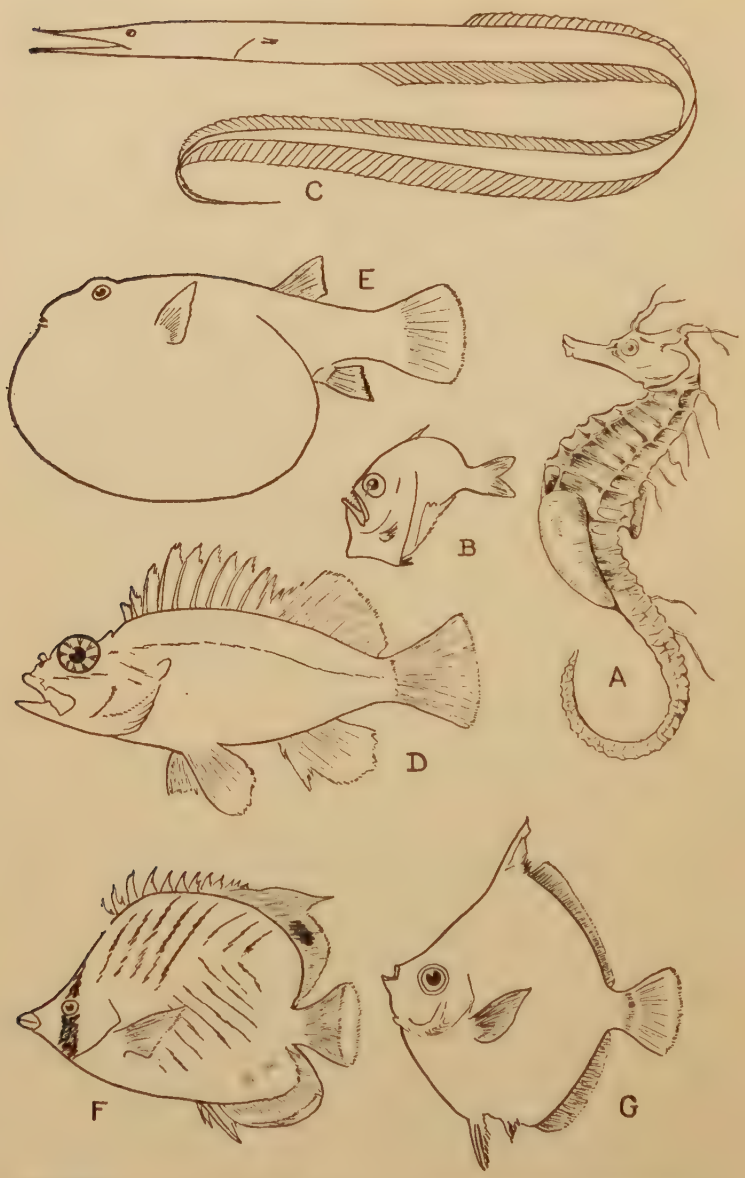


FIG. 18.—Some unusual styles of fishes. *A*, *Hippocampus*; *B*, *Sternoptyx*; *C*, *Serrivomer*; *D*, *Sebastopristis*; *E*, *Tetraodon*; *F*, *Chætodon*; *G*, *Antigonia*. (*A*, after Hilzheimer; *B* and *C*, after Goode and Bean; *D* to *G*, Hawaiian fishes.)

1. Elasmobranchii (Gristle fishes)

The fifty-seven genera of elasmobranchs in North America include about sixty species each of sharks and of rays. The sharks, dogfishes, and their allies, or the Selachians (Fig. 19, A and C), are active, graceful, elongated animals that prey upon other fishes. The rays, skates, guitar fishes, torpedoes, and their allies, on the contrary, are flattened, sluggish bottom feeders (Fig. 19, B).

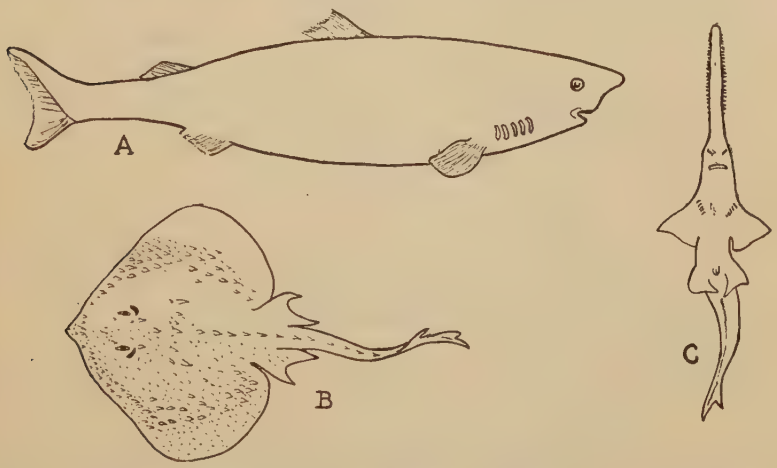


FIG. 19.—Elasmobranchs. *A*, nurse shark, *Somniosus; B*, a skate, *Raia,* (After Goode and Bean); *C*, a sawfish, *Pristis.* (After Boaz.)

Every elasmobranch may be distinguished by the following characteristics: (1) a mouth ventral in position rather than terminal; (2) openings of the gill slits separate and exposed, that is, not concealed behind a flap, as in other fishes; (3) a skeleton cartilaginous rather than bony, hence the common name "gristle fishes;" (4) placoid scales, that is, scales like tiny thumb tacks embedded in the skin, without shingling over each other as ordinary fish scales do; (5) a "spiral valve" in the intestine; (6) contour of the tail in side view showing two flanges, of which the dorsal one is the larger (heterocercal); (7) paired pelvic fins, which in the male are modified into "clasping organs;" and (8) the production of a relatively small number of eggs, that hatch and develop into considerable fishes within the oviduct of the mother before being born alive, instead of a prodigious number of uncared-for eggs broadcast in the water, as is customary with most fishes.

2. Holocephali

Existing representatives of the Holocephali are included in three genera, *Chimæra* (Fig. 20, A), "on the coasts of Europe and Japan, and the West Coast of North America and at the Cape of Good Hope;" *Callorhynchus* (Fig. 20, B), of south temperate regions; and *Harriota* (Fig. 20, C), in the deep sea.

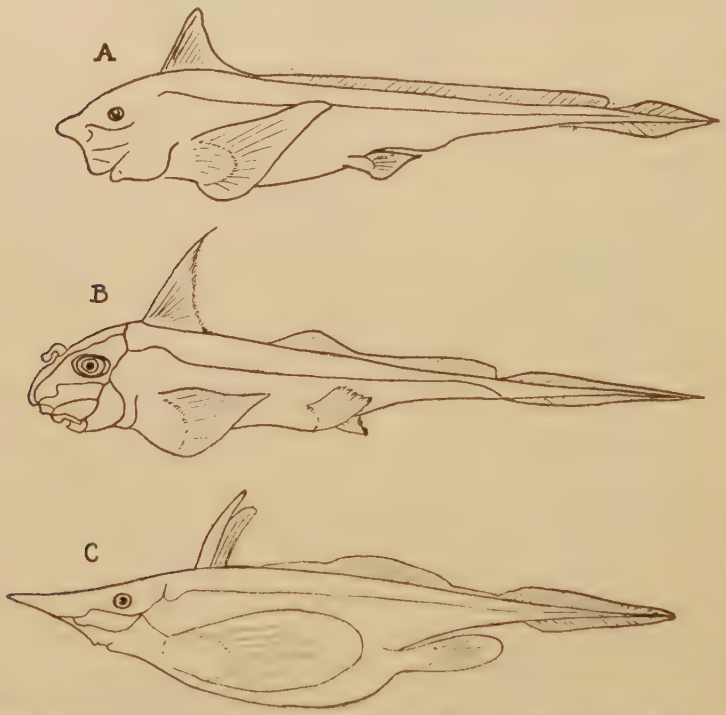


FIG. 20.—Holocephalan fishes. *A*, *Chimæra*; *B*, *Callorhynchus*; *C*, *Harriota*. (After Goode and Bean.)

The biological interest in these uncommon, bizarre "elephant fishes," or "spook fishes," lies in their intermediate anatomical position between sharks and rays, and other fishes. As in most elasmobranchs, the young are born alive, while the adults have a spiral valve inside the intestine, and possess a cartilaginous skeleton, although beginnings of bony formation appear in calcareous rings surrounding the persistent notochord.

The name *Holocephali* (*holos*, whole; *cephalon*, head) is given them because the upper jaw is immovably fused with the cranium

(autostylic) after the manner in higher forms, instead of being suspended indirectly by means of ligaments and cartilages (hyostylic), as in elasmobranchs. The gill slits are covered with a flap (operculum), as in higher fishes, and the tail, although heterocercal, has the dorsal flange of the caudal fin often elongated into a trailing filament.

3. Ganoidei

The living ganoids, or enamel-scaled fishes, represent the remnants of what was once the dominant type of fishes. These armor-

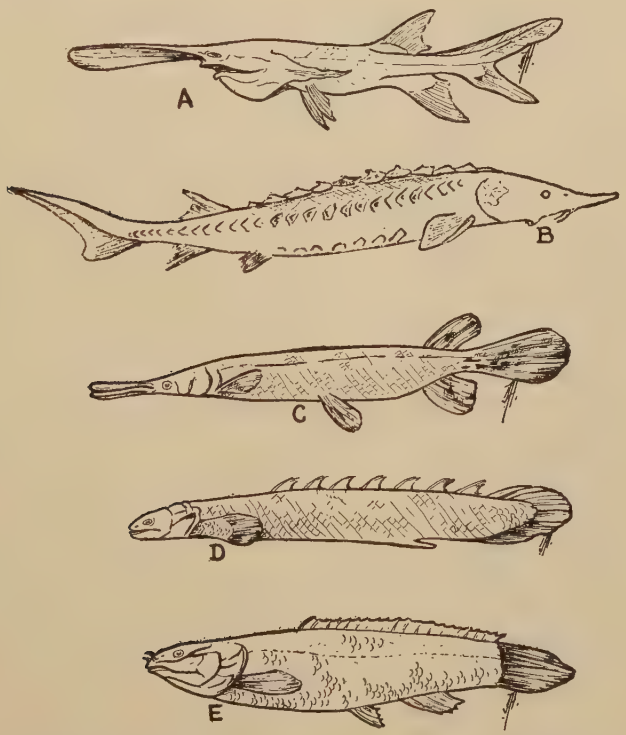


FIG. 21.—Ganoid fishes. *A*, *Polyodon*; *B*, *Acipenser*; *C*, *Lepisosteus*; *D*, *Polypterus*; *E*, *Amia*. (*A*, after Boaz; *C*, after Goode; *B*, *D*, *E*, from Newman, after Bridge.)

clads have given way before the more alert and less encumbered modern fishes, until today only eight genera and less than forty species, mostly fresh water forms removed from the fiercer competition of the more populous oceans, remain to tell the

tale of their own Golden Age, when hundreds of species and countless individuals of their kind lived and died in the vast Devonian seas.

The eight surviving genera of ganoids are the paddle-fishes, *Polyodon* of the United States (Fig. 21, A), and *Psephurus* of China; the sturgeons, *Acipenser* (Fig. 21, B), and *Scaphirhynchus;* the garpike, *Lepisosteus* (Fig. 21, C); *Polypterus* and *Callimoichthys*, of Africa (Fig. 21, D); and the bowfin, *Amia*, found in rivers and lakes of the United States (Fig. 21, E). Of these the first four are sometimes called "cartilaginous ganoids," because their skeletons, partly cartilage and partly bone, show a transition between elasmobranchs and bony fishes. The others, in which the cartilaginous components of the skeleton have been quite completely replaced by bone, are known as "bony ganoids."

FIG. 22.—The African lungfish, *Protopterus*, undergoing æstivation in the mud during the dry season. (After Hilzheimer.)

A further transitional condition is also shown by the presence of a degenerating spiral valve, along with the introduction at the same time of "pyloric cæca," which in higher fishes take the place of an elasmobranchian spiral valve as a device for enlarging the internal surface of the food tube.

Ganoids are either naked or clothed with peculiar enameled scales, which fit together edge to edge, rarely overlapping, like tiles around a fireplace. A single dorsal fin is usually located far posterior next to the tail, and there is present inside the body, a hydrostatic swim bladder.

4. Dipnoi

As the word *Dipnoi* (*di*, two; *pneuma*, air) indicates, the "lungfishes" have two ways of taking air, that is, by means of gills and by a modified swim bladder, or lung. They are semi-tropical fishes, dwelling only in countries where, instead of winter and

summer, a wet and dry season alternates. During the dry season they bury themselves in muddy pits (Fig. 22) and breathe air like land animals, but when the rainy season provides abundance of water they swim about and breathe through gills, fish-fashion. This passive method of bridging over a season of unfavorable dryness, is termed *æstivation*. Similarly, the term *hibernation* describes the habit of animals, like woodchucks and bears, which retire from activity during the cold winter season.

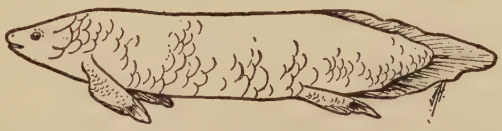


Fig. 23.—Australian lungfish, *Neoceratodus*. (From Newman, after Bridge.)

There are no lungfishes in North America, and only three living genera are known anywhere. These are *Protopterus*, in West Africa; *Neoceratodus*, in Australia (Fig. 23); and *Lepidosiren*, in Brazil (Fig. 24). They possess much interest for the zoölogist, not only from their peculiar habits and rarity, but because of the intermediate combination of their anatomical characters, which puts them in a class by themselves.

Fig. 24.—Brazilian lungfish, *Lepidosiren*. (From Newman, after Lankester.)

5. Teleostei

The *Teleosts* (*tele*, entire; *ost*, bone) are the true bony fishes. They constitute probably 90% of all known kinds of fishes. A simple way to determine a teleost is to eliminate its chances of belonging to any of the other classes already mentioned, consequently it will be unnecessary to dwell upon the diagnostic characteristics of this order here. A few representatives, out of the great variety of teleosts, are suggested by outline sketches in Fig. 18.

C. Amphibia

Amphibians (*amphi*, both; *bios*, life), like Dr. Jekyll and Mr. Hyde, typically lead a double life, that is, in the water and on the land, and thus as a class they bridge one of the greatest gaps in vertebrate evolution. The result of this ambitious attempt is that they present a medley of makeshift adaptations which leaves them still a long way from vertebrate perfection but, nevertheless,

makes them particularly beguiling to the student of comparative biology.

There are certain dual conditions that any animal, living part of the time submerged in water and part of the time upon land, must meet. For example, *locomotion* calls for an entirely different set of organs in the two cases. In water an elongated fishlike body, propelled by a muscular tail, has proved to be the most efficient mechanism of locomotion, while on land such an arrangement would be out of the question, because in thin air a propeller that could develop power enough to move the body at all would necessitate so great an addition of heavy muscles as to defeat at once the possibility of easy locomotion. When the weight of the body is no longer supported by the surrounding medium of water, legs appear, acting as levers to lift the body away from frictional contact with the ground, and it is quite possible to equip these levers with muscles enough for their successful operation without adding excessively to the entire weight to be moved.

The amphibians, beginning with the fishlike tadpole stage in water and ending, let us say, with the awkward, slow-moving toads on land, exhibit a series of locomotor adjustments of wide range. The legs of salamanders are ridiculously small and inadequate. They do not even lift the body from the ground, since, instead of being directed ventrally as supports, they project laterally, and may be used only slightly in poling the wriggling body along over the ground. Even in frogs and toads, where amphibian legs reach their highest development, the legs are so inefficiently anchored to the supporting backbone, that these animals cannot bear their weight upon them in the sustained manner necessary for standing or walking, and can progress only by the momentary exertion of hopping or jumping. When not locomoting they never stand but always sit.

Again, *breathing* calls for a different equipment under water and in the air. The essential feature of every breathing device is a delicate wall, or membrane, separating blood from oxygen. In water animals *gills*, which are thin-walled structures containing blood and hanging in surrounding water in which oxygen is dissolved, fulfill this condition. However, when exposed for any considerable time to air, thin-walled gills may dry up and collapse, making gaseous exchange no longer possible. The consequence is that, in animals breathing air, *lungs* are developed. These are

enclosed sacs, in which an enormous expanse of capillary blood vessels behind very thin walls is exposed continuously to air, but in which drying up and collapse of the thin, moist walls is prevented because of the relatively small openings of the lungs to the outside, through which evaporation can occur. Amphibia not only utilize gills and primitive lungs but they also breathe to a large extent directly through the *skin*, which, so long as it is kept moist, may remain thin enough to serve as the membrane separating blood from air. This enforced diversity of mechanisms for breathing has made perfection of any one device impossible. As a result amphibians are such poor breathers that they cannot develop heat enough to maintain a body temperature independent of that of their surroundings. This makes them "cold-blooded" and, since they can never be active when it is cold, they are consequently excluded entirely from frigid regions, while in the temperate zones where winter condemns them to hibernation, they can exercise seasonal activity for only part of the time.

Furthermore, the *metamorphosis* of such an amphibian as a toad, necessitated by its emergence from life in water to land, works profound changes in its structure and feeding habits. During its lifetime the toad uses in succession six different kinds of food. First, while in the egg, it absorbs the *yolk* stored therein; then, upon hatching, it develops a temporary mouth and eats its way out through the "*jelly*" of the egg envelopes. Next, it becomes a free tadpole, swimming about by means of its locomotor, fish-like tail, and feeds upon *vegetation* in the water, but, as the growth pains of its coming transformation approach, it loses its temporary mouth, and, along with it, the appetite for vegetable food. Tiny legs and arms now sprout out, and, instead of swimming about so much, the little toad sits quietly in its shirt sleeves and devotes itself introspectively to the task of changing over its *tail* into body substance. By this time cold weather is approaching and it goes into a long winter retirement, during which its only food is the "*fat body*," a peculiar nutritive organ attached to the intestine within the body cavity and destined to meet the demands of hibernation. Finally, with the warmth of returning spring, the young toad, now equipped with a permanent mouth and a marvelous lassoing tongue, emerges into a life of activity upon land, catching *insects* for a living.

It is not very difficult to recognize an amphibian, although, by

the uncritical, this group is sometimes confused with the Reptilia, from which it was distinguished as an independent class in 1801 by Brogniart. Amphibia are characterized by primitive legs, terminating in fingers and toes without claws, and by a moist, scaleless skin. The skull articulates with the first vertebra at two points (occipital condyles), instead of one as in reptiles and birds, and the *sacrum*, or that part of the vertebral column to which the hind legs are attached, consists of but a single vertebra. The young all breathe by means of gills.

Living Amphibia may be arranged in three orders:—APODA, URODELA, ANURA, and to these may possibly be added the extinct order, STEGOCEPHALI.

1. Stegocephali

This latter group, which, according to fossil remains, bears a resemblance to living Amphibia, disappeared from the earth before any known representatives of modern amphibians made their appearance, a fact, as pointed out by Jaekel, that is embarrassing for those naturalists who maintain that the Stegocephali are ancestors of recent amphibians. The gap that separates these similar animals, however, may sometime be filled by the discovery

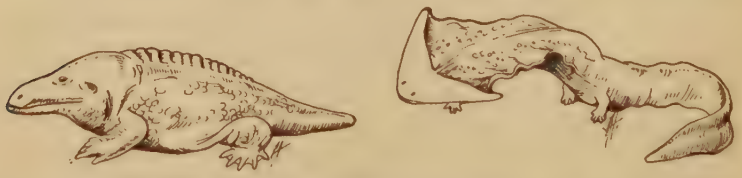


FIG. 25.—Restorations of extinct Stegocephali, according to Gregory and Deckert. (After Newman.)

of intermediate fossils. The Stegocephali flourished in the swampy Carboniferous Age, along with giant rushes and mosses, before there were any birds, insects, or flowers, and when the hot steamy atmosphere was laden with an abundance of carbon dioxide. They were the earliest four-footed air-breathers, large awkward creatures clothed with an armor of scales, and with a brain so small that it could have been pulled out through the *foramen magnum* at the back of the skull (Fig. 25). The reason for naming them Stegocephali (*stegos*, roof; *cephalon*, brain), or "roof-brained," is because the size of the skull by no means indicates the cranial capacity of these stupid beasts, there being a large, vacant, attic-

like space roofed in above the cranium proper, or that part of the skull in which the insignificant brain was housed.

2. Apoda

Of modern Amphibians the *Apoda* are the least familiar. They include tropical forms from Africa, South America, Ceylon, and India, which burrow in the ground. In appearance they resemble worms, although possessing a vertebral column and numerous other characteristics which place them unmistakably with the Amphibia. As examples of the order may be cited the "blind cæcilian" of West Africa, *Cæcilia* (Fig. 26), and *Ichthyophis*, of Ceylon (Fig. 31, C).

Fig. 26.—A tropical wormlike amphibian, *Cæcilia*, partly out of its burrow. (From Newman, after P. & F. Sarasin.)

3. Urodela

The *Urodeles* (*uro*, tail; *dela*, visible) are the salamanders, newts, and mud puppies. They retain their tadpole-like tail throughout life, and most of them never emerge from life in water, although some do so, living under rotten logs and in similar damp situations.

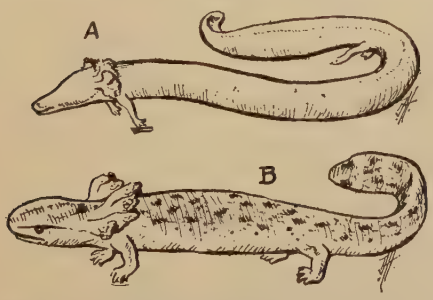


Fig. 27.—Perennibranchiate urodeles. *A*, *Proteus*, a blind "olm" from German caves; *B*, *Necturus*. (From Newman, after Lankester.)

Urodeles may be arranged in three subclasses: the PERENNIBRANCHIATA; the DEROTREMATA; and the MYCTODERA. The *Perennibranchiata* never lose their gills. They include the "olm," *Proteus* (Fig. 27, A), a blind, practically pigmentless salamander which lives in the waters of certain caves in southern Europe, and is famous from the fact that it has the largest known red blood corpuscles of any vertebrate; *Typhlomolge*, another blind cave-dweller in Texas; and the "mud puppy," *Necturus* (Fig. 27, B), which is found from the Mississippi Valley eastward. The *Derotremata* lose the gills when adult, but one pair of gill slits usually persists. Representative forms are the "mud eel," *Siren* (Fig. 28, A),

of the rice fields of southern United States, whose long, snake-like body and uncanny appearance secure for it immunity from human interference quite out of proportion to its harmless character; the "Congo snake," *Amphiuma* (Fig. 28, B), from southern United States, which is not a snake at all; the "hellbender," *Cryptobranchus* (Fig. 28, C), inhabiting the Ohio River and its tributaries; and the "giant salamander," *Megalobatrachus*, of Japan, which sometimes attains a length of over five feet.

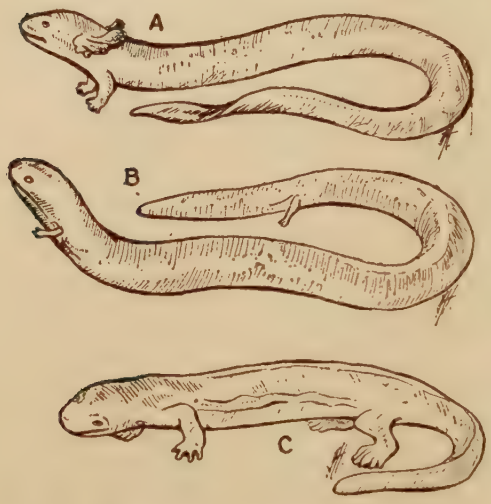


FIG. 28.—Derotreme urodeles which lose their gills when adult but usually retain one pair of gill slits. *A*, "mud eel," *Siren*; *B*, "Congo snake," *Amphiuma*; *C*, "hellbender," *Cryptobranchus*. (From Newman, after Lydekker.)

The *Myctodera*, whose gills in the adult stage not only disappear but whose gill slits become entirely closed, embrace the newts and true salamanders. Some of the better known genera are *Triturus* (Fig. 29, A), the "vermilion spotted newt" of the ponds and streams of New England; *Desmognathus* (Fig. 29, B), which hatches its small rosary of eggs upon land; *Eurycea* (Fig. 29, C), *Plethodon* (Fig. 29, D), and *Ambystoma* (Fig. 29, E), all contact-lovers to be found under bark, logs, and stones near the American streams in which they breed; the dainty Alpine salamander, *Triton*, whose fancifully frilled tail, in the case of the male (Fig. 29, F), serves as a wedding garment during the breeding season; and *Salamandra*, which includes the true salamanders of the Old World.

The "black salamander," *Salamandra atra*, of Switzerland, is particularly adapted to life in the cold and tumultuous waters of the glacial streams where it lives. Its eggs, only two of which develop at a time, are protected and prevented from being washed away, by remaining within the oviduct of the mother, where they

hatch and pass through their entire tadpolehood to a sufficient size to insure their safety, before they are born at all.

4. Anura

The *Anura* (*a*, without; *ura*, tail) are the frogs, toads, and tree frogs, who lose their tails before becoming adult. They are the

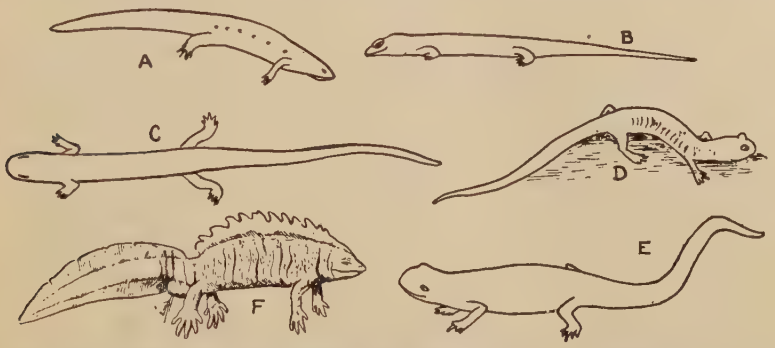


FIG. 29.—Newts and true salamanders, Myctodera. *A*, *Triturus*. (After Ditmars.) *B*, *Desmognathus*. (After Dunn.) *C*, *Eurycea*. (After Dunn.) *D*, *Plethodon*. (After Ditmars.) *E*, *Ambystoma*. (After Kingsley.) *F*, male *Triton*. (After Hilzheimer.)

first vertebrates to become vocal, since the other Amphibia, as well as fishes (with the exception perhaps of the "grunters" that make a noise by expelling air from the swim bladder), are silent. These quaint and cheerful singers, moreover, are the first animals that have movable eyelids and a lacrimal gland, and so are enabled to wink and to shed tears. This does not mean that trouble enters the world for the first time with them, since tears and blinking are primarily adaptations for keeping the eyes of land animals clean, rather than machinery for the expression of the emotions.

FIG. 30.—A tree frog, *Hyla*. (After Dickerson.)

There is but one common genus of toads in North America, *Bufo*, although there are many genera in other parts of the world, particularly in South America. Some years ago the Department of Agriculture in Washington, in a pamphlet upon the economic value of the common toad, *Bufo americanus*, estimated

that a single individual in a garden was worth $19.44 as an insect destroyer. No doubt with the changing value of the dollar, and the high cost of living following the war, this figure should now be in-

FIG. 31.—Care of young among Amphibia. *A*, nests of *Hyla faber* built of mud. (After Wiedersheim.) *B*, *Rhacophorus schlegeli* of Japan in amplexation within a hole in a muddy bank of a stream. The eggs are deposited in a mass of foamy mucus, and washed out into the stream below by the rain. (After Wiedersheim.) *C*, an Apodan, *Ichthyophis glutinosa*, guarding its eggs. (After P. & F. Sarasin.) *D*, the "nurse frog" of Europe, *Alytes obstetricans*. The male carries strings of eggs attached to its hind legs. (After Cope.) *E*, *Hyla gœldii*, with eggs glued to back of female. (After Ihring.) *F*, *Nototrema pygmæum*, female with dorsal brood pouch containing only a few large eggs. (After Brandes and Schoenichen.) *G*, South American toad, *Pipa dorsigera*, the eggs of which are deposited in pits upon the spongy back of the female by means of the everted cloaca, that serves as ovipositor, where they remain until the metamorphosis of the tadpoles into tiny toads. (After Bartlett.) *H*, *Rhinoderma darwini*, section of head region showing eggs carried within the vocal sac, the position of which when inflated is represented by the dotted circle. (After Wiedersheim.) *I*, *Arthroleptis seychellensis*, the tadpoles of which are transported to fresh pools by being attached to the back of the male. (After Brauer.)

creased. *Bufo fowleri*, the second of two species of toads in eastern North America, is distinguishable by a white unspotted belly, instead of a yellowish spotted belly like that of *Bufo americanus*, also by the fact that it is to be found in sandy places near the seashore.

The commonest genus of frogs is *Rana*, several species of which are found in North America and Europe. *Scaphiopus*, is the American spadefoot frog.

The little tree frogs have adhesive discs at the ends of their fingers and toes that enable them to climb trees, where they conceal themselves and persistently send out their ventriloquistic calls. American genera are:—*Acris*, the "cricket frog"; *Pseudacris*, the "swamp tree frog"; and *Hyla*, the common tree frog (Fig. 30).

Many Amphibia are remarkable for the ways in which they care for their eggs and young. Some examples are brought together in the accompanying table, and are in part illustrated in the sketches on page 36 (Fig. 31, A–I).

EXCEPTIONAL INSTANCES OF CARE OF THE YOUNG AMONG AMPHIBIA

I. Protection by means of nests or nurseries
  1. Enclosures of mud in water..... *Hyla faber* (Brazil)
  2. Resin-lined rain-water holes in trees..... *Hyla resinifictrix* (Brazil)
  3. Holes, filled with foam produced by the parents, in banks over streams..... *Rhacophorus schlegeli* (Japan)
  4. Glued to folded leaves overhanging the water *Phyllomedusa hypochondrialis* (Paraguay)
  5. In jelly-enveloped overhanging twigs *Rhacophorus reinwardtii* (Java)

II. Direct nursing by parents
  1. Eggs protected by coiling around them
    A. In holes in damp earth..... *Ichthyophis glutinosa* (Japan)
    B. Under logs and stones..... *Plethodon* (United States)
  2. Eggs carried about by parents
    A. Around the neck..... *Desmognathus fusca* (United States)
    B. Around the hind legs of the male *Alytes obstetricans* (Germany)
    C. Glued to back of female.... *Hyla gœldii* (South America)
    D. Glued to belly of female. *Rhacophorus reticulatus* (Ceylon)
    E. In the dorsal pouch of female *Nototrema pygmœum* (Venezuela)
    F. In separate pits on back of female *Pipa dorsigera* (Surinam)
    G. In the mouth cavity of female..... *Hylambates brevirostris*
    H. Within the vocal sacs of male. *Rhinoderma darwini* (Java)

III. Tadpoles transported to fresh pools
  A. By attaching to male *Arthroleptis seychellensis* (Seychelles)
  B. By attaching to female..... *Hylodes lineatus*

IV. Tadpoles kept within the oviduct until after metamorphosis, i. e., viviparous.... *Salamandra atra* (Switzerland)

D. Reptilia

Reptiles (*repere*, to crawl) are named after the highly specialized, legless, crawling snakes, but include also the lizards, turtles, alligators, and *Sphenodon* of New Zealand, as well as a vast company of forms now extinct, many of them gigantic, which dominated the Mesozoic world throughout a dynasty that endured for ages. They are the first vertebrates that are definitely committed to life on land. This is true even of alligators, turtles, and water snakes which, although spending much of their time in water, come out upon land to lay their eggs. Their young never pass through an aquatic larval stage.

Some of the characteristics distinguishing Reptilia from Amphibia are (1) a scaly skin, with very few glands, adapted to conserve water necessary to life on land within the body tissues; (2) gills that are never functional, and post-embryonic breathing that is always accomplished by means of lungs, into which air is drawn (except in turtles) by action of rib muscles. [In Amphibia there are no movable ribs nor rib musculature, so that air has to be forced into the lungs by the muscles of the throat. This method of swallowing air is also employed by the turtles whose ribs are flattened and joined into a solid box that prevents any bellows-like movement on their part.] (3) Possession of claws whenever fingers and toes are present; (4) one occipital condyle instead of two; (5) slow long-continued growth, and great longevity; (6) internal fertilization of relatively few large eggs, with modifications necessary for accomplishing this end; (7) the possession of an *amnion* and *allantois*, two temporary embryonic structures, appearing for the first time in reptiles, and present also in birds and mammals. These structures are necessary because the young animal no longer accomplishes its transformation from the egg in water, as do fishes and amphibians, but within an eggshell, upon land, or, in the case of mammals, within the uterus of the mother.

The astonishingly rapid growth of any developing embryo, which can be realized only by those who have closely observed it, necessitates cells and tissues of extreme delicacy, not encumbered with adaptations for withstanding exposure to dry air or to mechanical shocks. In the growing embryos of fishes and amphibians, this delicacy and pliability is made possible by the surrounding medium of water in which they are immersed. With the con-

querors of the land, however, the developing embryo can no longer be cradled in open water, and so the protective *amnion* develops around the embryo to take the place of it. This is a thin enveloping sac, filled with a secreted, watery, amnionic fluid in which the growing embryo floats, so that after all it may be said that, in a certain sense, every vertebrate passes its early life submerged in water.

The *allantois* is a temporary breathing and excreting organ, made necessary by the fact that when an egg is not laid in water but upon land, it must be enclosed within a shell which will prevent its drying up. This emergency organ, bearing a rich network of blood vessels, grows out from the digestive tube of the embryo and enwraps it, amnion and all (Fig. 32). It lies close against the thin egg membrane (*chorion*) so that through it and the porous eggshell, there is effected the interchange of gases between the blood and the outside world, essential in breathing. In the case of mammals, where the egg has no shell, but develops into a fetus that is parasitically attached to the uterine walls of the mother, the capillary-laden allantois comes into intimate interdigitating contact with the richly vascularized wall of the uterus, to form the *placenta*, and it is through this organ that the young animal breathes until it is born into respiratory independence.

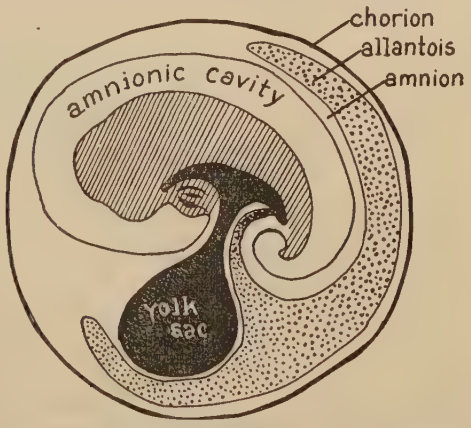


FIG. 32.—Diagram of the relation of amnion and allantois to the embryo.

1. Extinct Reptiles

Extinct reptiles wrote, with their fossil remains, a long and dramatic chapter in the history of the earth for modern intelligent man to read. Several entire orders, the flying *Pterodactyls*, aquatic *Ichthyosaurs*, and long-necked *Plesiosaurs*, for example, have, so far as is known, left no living descendants, but the *Dinosaurs*,

noblest of them all, were probably the ancestors of modern lizards, as well as possibly of birds and mammals.

During the Golden Age of Reptiles (Mesozoic), that lasted,

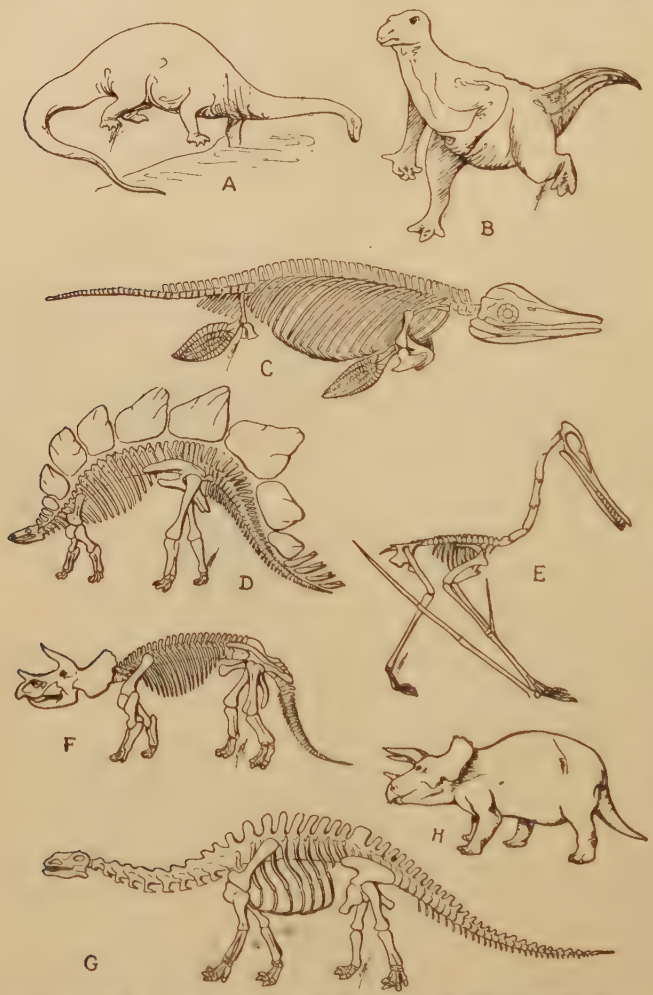


FIG. 33.—Various extinct reptiles, selected to indicate diversity of form. They are not drawn to a common scale, but are mostly gigantic in size. *A*, restoration of *Diplodocus*. (After Smit.) *B*, restoration of *Iguanodon*. (After Heilman.) *C*, *Ichthyosaurus*. (After Conybeare.) *D*, *Stegosaurus*. (After Marsh.) *E*, *Pterodactylus*. (After Seeley, but according to Abel in incorrect quadrupedal attitude.) *F*, *Triceratops* skeleton. (After Marsh.) *G*, *Brontosaurus*. (After Marsh.) *H*, restoration of *Triceratops*. (After Nuhn.)

according to some geologists, for 7,000,000 years, these ruling animals attained a great diversity of form and adaptation which enabled them to live in a variety of habitats, such as trees, water, swamps, dry land, and even air. Some flesh-eating dinosaurs, for example, developed large, powerful hind legs which helped them to leap after their prey, while the more stolid plant eaters were underpinned by four massive, pillar-like supports of more nearly equal size. Many of them grew to dimensions so gigantic that elephants would seem like dwarfs beside them. The imagination is sure to be thrilled by a picture of the Mesozoic landscape with its weird reptilian inhabitants. Some of these strange creatures of past pre-camera days are suggested by the sketches on page 40 (Fig. 33, A–G).

Modern reptiles may be grouped into four orders:—RHYNCHOCEPHALIA, CROCODILIA, CHELONIA, and SQUAMATA.

FIG. 34.—A primitive New Zealand lizard, *Sphenodon*. (From Hilzheimer, after Berg.)

2. Rhynchocephalia

The *Rhynchocephalia*, which include many fossil kinds, are represented today by a single surviving species, *Sphenodon*, of New Zealand (Fig. 34). Reference has already been made (page 2) to the "third eye" of this interesting "old curiosity shop" of ancestral peculiarities.

3. Crocodilia

The *Crocodilia*, likewise with many fossil relatives, include the *crocodiles*, of India, China, the West Indies, Africa, and the Malay Archipelago; the broad-snouted *alligators* of the Mississippi Basin and China (Fig. 35); the *caimans* of Central and South America; and the narrow-snouted *gavials* of the Ganges in India. They are all inhabitants of tropical or semi-tropical rivers, clumsy and stiff-necked on land but quite at home in shallow water, where their powerful tails, which are compressed laterally, enable them not only to swim forward but to strike powerful side blows.

FIG. 35.—*Alligator*. (From Newman, after Ditmars.)

4. Chelonia

The *Chelonia* are turtles and tortoises, modified "reptiles in a box," which have gone in for the principle of defense so extensively that they have come to resemble the "tanks" of modern warfare. Even the toothless jaws are encased in a horny beak, like that of birds, while the only flexible parts of the backbone of these animals are the neck and the insignificant tail.

Some genera of turtles are *Dermochelys*, the "leatherback," and *Coretta*, the "loggerhead," which cruise about in salt water, and may attain a weight of several hundred pounds; *Chelonia*, the "green turtle," also a seagoing animal and prized as food; *Chelydra*, the "snapper"; *Amyda*, the "soft-shell" (Fig. 36); *Pseudemys*, the "terrapin," and delight of epicures; *Testudo*, the long-lived giant of the Galapagos Islands; *Eretmochelys*, the "hawksbill," from which "tortoise shell" is obtained; *Clemmys*, the wood turtle; *Kinosternum*, the mud turtle; *Terrapene*, the "box turtle," that is able to withdraw its head entirely, and to close the door with a hinged lid; and the small, beautifully decorated "painted turtle," *Chrysemys*. America, of all continents, is particularly rich in chelonial inhabitants.

Fig. 36.—A soft-shelled turtle, *Trionyx*. (After Hilzheimer.)

5. Squamata

The *Squamata* are reptiles clothed with a great number of regularly placed scales which cannot be separately detached like the scales of bony fishes but are connected together into a continuous armor. They comprise two suborders: the *Sauria*, or lizards, and the *Serpentes*, or snakes, distinguished from each other by the fact that the former have movable eyelids and visible ear pits, while the latter do not, and because the lizards are unable to open the mouth in the comprehensive manner which makes it possible for snakes to swallow living prey larger in diameter than their own bodies.

Fig. 37.—A "gecko" from Madeira, with adhesive toes, showing a regenerating tip to the tail. (After Saville-Kent.)

The *Sauria*, or lizards, are typically sun worshippers, dwelling in regions of much sunshine and, for the most part, avoiding water.

A notable exception is the water lizard, *Amblyrhynchus*, which is abundant on the rocky shores of the Galapagos Islands. The "geckos" of the Malay region and the Mediterranean have adhesive toes that enable them to clamber about with great agility after flies, in trees and upon the walls of houses (Fig. 37). *Draco*, of India, the "flying dragon" (Fig. 38), is able to volplane from branch to branch of the trees it inhabits by means of a capelike expansion of the skin on its arms. *Iguana*, a large arboreal Mexican lizard of fierce aspect but harmless character, is regarded as good to eat, while the largest lizard of all belongs to the genus *Varanus*, of Africa, the East Indies, and Australia. The *Chameleon* (Fig. 39), with wonderfully prehensile tail and grasping feet, and a Joseph's coat of many colors, is a native of

FIG. 38.—An Indian lizard, *Draco*, the "flying dragon." (After Hilzheimer.)

FIG. 39.—An African lizard, *Chameleon*, which has a long extensile tongue and is famous for its power of changing color. (After Hilzheimer.)

Africa, although its name is sometimes inaccurately applied to the little American *Anolis* (Fig. 40), of changeable colors, which inhabits the canefields of the south, and preys upon the insects that are

attracted to the sweet juices of the cane. *Ophisaurus*, the "glass snake," and *Amphisbæna*, the "slow-worm," are legless lizards which, although snakelike in appearance, have the non-dilatable mouth, visible ear pits, and movable eyelids of true saurians. *Lacerta*, of many species, is a very common genus of the Old

FIG. 40.—An American "chameleon," *Anolis*. (After Ditmars.)

World; while *Scleoporus*, the "swift," and *Plestiodon*, the "skink," are New World representatives. In the desert region of the Southwestern United States is found the grotesque "horned toad," *Phrynosoma* (Fig. 41), that is called a toad only by the indiscriminating, as well as the "Gila monster," *Heloderma* (Fig. 42), an ugly black and orange beast with a large, round, stubby

FIG. 41.—The "horned toad," *Phrynosoma*, of the desert region of southwestern United States. It is not a "toad" but a lizard. (From Hegner, after Gadow.)

tail, wherein is stored reserve fat. *Heloderma* has the unenviable distinction of being the only known lizard whose bite is venomous.

The *Serpentes* are the legless snakes, described by Ruskin as "a wave but without wind, a current but with no fall." They walk upon their ribs, or "jerk themselves forward by a rapid straightening of their sinuous curves" (Thomson). The curious arrangement of their internal organs has direct reference to their external architecture. The body cavity is so elongated that the

intestine is comparatively uncoiled, while the liver is long and attenuated with the bile sac behind instead of beside it, and the kidneys also slender and placed one behind the other. All the

FIG. 42.—"Gila monster," *Heloderma*, the only known venomous lizard. (From Newman, after Lydekker.)

FIG. 43.—Texas rattlesnake, *Crotalus*. (After Stejneger.)

organs are arranged in tandem fashion, and only one long narrow lung develops, although the stub of the other remains.

Most of the snakes are beneficial animals, feeding largely upon injurious insects and small rodents, although they have suffered vicariously from an unsavory reputation ever since one of their number took part in the original eternal triangle play in the Garden of Eden. Of about 110 species in the United States, less than twenty are venomous. The worst of these, so far as man is concerned, are the rattlesnakes, *Crotalus* (Fig. 43), of several species; the "copper-head," *Agkistrodon mokasen*, and the "water moccasin," *Agkistrodon piscivorus*, of the South. The "black snake," *Boscanion;* the "puff adder," *Heterodon;* the "milk snake," *Lampropeltis*, and the "garter snake," *Thamnophis*, are among the common harmless varieties.

E. Birds

All birds have feathers. This one conspicuous characteristic suffices to identify a bird, even to a child, for no other animals have feathers. Since the vertebrate type probably reaches its highest specialization, along certain directions at least, in the birds, it is not at all difficult to find many other distinguishing characteristics of this familiar and much studied class of animals.

The secret of the anatomical peculiarities of birds, lies in their

adaptation to flight in the air. The same combination of organs, which in a fish is modified into a living submarine, and in a reptile becomes adapted to a life of prevailing contact with the earth, is transformed in a bird into a flying machine heavier than air. The skeletal framework of a bird, comparable bone by bone with that of other vertebrates, becomes compacted together or centralized, thus affording the smallest possible bulk to pass through the air, although the surfaces of individual bones remain expansive for the attachment of the necessary voluminous muscles of flight. In case of the breastbone, the humeral heads, and the sacro-pelvic complex particularly, the surfaces are notably increased beyond those of other vertebrates. Every part of a bird that can possibly do so, moves from the anatomical suburbs into the compact urban district of the body. For example, considerable weight is shifted from the periphery to the center within the compact body when the dense, heavy teeth, commonly found in the head of other vertebrates, have been replaced by a light, horny beak, while a tough, muscular, central gizzard, lined with grinding stones, does the work which teeth once did in ancestral birds. The heavy, trailing, reptilian tail has telescoped into a degenerate skeletal stub, thus centralizing weight, while in place of it a secondary tail of light, air-resisting feathers, is added to be used as a rudder in flight. The presence in birds of such a bony tail, composed of many foreshortened vertebræ instead of a single larger bone which might have better served as a support for the tail feathers, is one of the numerous evidences of reptilian ancestry. In fact, someone has happily described birds as "glorified reptiles."

The bones of a bird are not only compact but are lightened and made appropriate parts of a flying machine by being hollowed out to the limit of mechanical safety. Furthermore, bodily weight is partially counterbalanced by the development of numerous air sacs, that grow out from the lungs, and come to occupy all available spaces between the internal organs, even extending to the cavities of the hollow bones. The light feathers also, which clothe a bird, hold a considerable blanket of enveloping air around the body that no doubt, like a pneumatic life preserver, adds much to its buoyancy. Moreover, the large intestine, particularly the rectum where, in other vertebrates the feces are carried, is very much reduced in length. Flying animals cannot afford to be weighted

down with any excess fecal baggage, and so, not having suitable provision for its storage, birds promptly get rid of it.

Since the entire support of a bird's body when not in flight devolves upon the hind legs alone, the fore legs are emancipated from service as legs, and are left free to become expansive wings for flight. The fore legs, or arms, are thus entirely given over to flight, and cannot be used for the capture and manipulation of food, therefore the head necessarily becomes prehensile by being mounted upon an extremely flexible neck and equipped with a forceps-like beak for picking up food. It will be noted that the remarkably well-developed eyes, located on either side of the beak of a bird, are much nearer their work than the eyes of any other animal which reaches for its food in a fashion unlike that of a bird.

Fig. 44.—The oldest known bird, *Archæopteryx*, showing teeth, three fingers, feathers, and a lizard-like tail. The Berlin specimen. (After Parker and Haswell.)

The excessive activity involved in flight has been met in birds by a relatively larger heart than other animals possess and by a particularly effective respiratory apparatus, which so increases the warmth of the body as to render it constant regardless of the surrounding temperature. As a result birds are active the year around, in cold as well as in warm weather, and never become sluggish or obliged to hibernate, as "cold-blooded" animals do, but rise above the handicaps of temperature and climate, even migrating to distant and more congenial localities, whenever occasion demands it.

1. Fossil Birds

On account of their light bones and the rapid destruction of their bodies after death, birds do not lend themselves readily to fossilization, and, therefore, do not present so extensively a re-

corded story of past achievements as the reptiles. The earliest known trace of bird life is the imprint of a single tail feather, discovered in the Jurassic slate of Bavaria. This unmistakable fragment dates back to the middle of the long Age of Reptiles, long before mammals had risen to become a power upon the earth. In splitting up the finegrained lithographic stone from the deposit of the Solenhofen quarry in Bavaria, from which came this

FIG. 45.—A toothed bird, *Ichthyornis*, with keel on the breastbone, from Kansas chalk beds. (After Marsh.)

priceless first known feather, there were found also at different times two entire skeletons, crushed flat and embedded within the slate, of the kind of birds that doubtless produced this famous tail feather. From these slight but convincing remains, the species of this oldest of all known birds was named *Archæopteryx lithographica*. *Archæopteryx* (Fig. 44) was about as large as a crow; had lizard-like teeth set in sockets in the jaws; a long uncentralized bony tail; three fingers with claws terminating each wing, instead of one finger, as modern birds have; and FEATHERS.

The chalk beds of western Kansas, which were laid down at a

much later date than the Bavarian slates of Jurassic times, have yielded the fossil remains of other ancient birds with teeth, for example, *Ichthyornis* (Fig. 45), in form like a tern, and *Hesperornis* (Fig. 46), a flightless swimming bird somewhat like a penguin, of which over one hundred specimens have been found.

2. Modern Birds

Excluding *Archæopteryx*, which is a connecting link in a group by itself, and the ancestral toothed birds of Kansas, modern

FIG. 46.—A toothed penguin-like bird, *Hesperornis*, without a keel on the breastbone, from Kansas chalk beds. (After Marsh.)

FIG. 47.—A primitive wingless burrowing bird, *Apteryx*, from New Zealand. (Drawn from a specimen in the collection at Brown University.)

birds may be grouped in two subclasses, RATITÆ and CARINATÆ, based upon the ability to fly.

The *Ratitæ*, none of which are natives of North America, are running birds that cannot fly. They include ostriches, cassowaries, emus, rheas, and the curious wingless "kiwi," *Apteryx* (Fig. 47), of New Zealand, which has survived the perils of a hostile world, in the absence of ability to escape by flight, by

Fig. 48.—A giant "moa," *Dinornis*, from a mounted specimen eighteen feet in height in the exhibit of the Government of New Zealand at the Panama-Pacific Exposition. (Drawn by H. R. Meyers.)

burrowing in the ground. In New Zealand also, that land of ancient curiosities, have been found abundantly the remarkable fossil remains of the largest of all birds, the "moa," *Dinornis* (Fig. 48), which reached a height of at least eighteen feet. It is likely that this species of gigantic ostrich-like birds has become extinct within the memory of man, for the native Maoris of New Zealand, when they first came into communication with the white settlers, had legends about these birds that had been handed down to them from their fathers.

The *Carinatæ* are flying birds, whose wide breastbone has developed an expansive keel for the attachment of muscles of flight. According to Gadow the Carinates comprise thirteen *orders* as named below. More or less familiar examples are given to represent each order.

1. COLYMBIFORMES—loons, grebes.
2. SPHENISCIFORMES—penguins.
3. PROCELLARIIFORMES—petrels, albatrosses.
4. CICONIIFORMES—pelicans, cormorants, herons, flamingoes, storks.
5. ANSERIFORMES—geese, ducks, swans.
6. FALCONIFORMES—vultures, hawks, eagles, condors.
7. TINAMIFORMES—tinamous.
8. GALLIFORMES—turkeys, quail, fowls.
9. GRUIFORMES—rails, and other marsh birds.
10. CHARADRIIFORMES—plover, sandpipers, and other shore birds, gulls, terns, puffins, auks, pigeons, doves.

11. CUCULIFORMES—cuckoos, parrots.
12. CORACIIFORMES—kingfishers, owls, whippoorwills, swifts, hummingbirds, woodpeckers.
13. PASSERIFORMES—flycatchers, and singing birds.

F. Mammals

The first mammals to appear on earth were small and insignificant contemporaries of the gigantic reptiles of the Mesozoic Age. As long as huge carnivorous dinosaurs held sway, the modest little mammals, probably largely arboreal in habit, kept out of the way and bided their time. Perhaps they hastened that time somewhat by feeding upon the eggs of their terrifying enemies while eluding capture themselves. At any rate it is certain that, in the long struggle for "a place in the sun," it has been wits rather than brute force that has enabled mammals to outdistance their competitors.

No doubt the mechanism which insures "warm-bloodedness," that is, a constant bodily temperature independent of changes in the surroundings, has had much to do with the conquest of the earth by mammals, since by reason of this important characteristic they have been able to establish themselves not only throughout temperate areas and the humid tropics, but even in dry deserts and frigid polar regions.

FIG. 49.—Sketch of a field mouse, reduced to one-half actual size. To represent the outline of a whale drawn to the same reduced scale would require a page forty feet wide.

While the highly specialized birds have sacrificed everything to developing the power of locomotion by flight in air, the mammals have chosen the better part of improvement along the line of the nervous system. Doubtless it is this achievement that has been the greatest of all factors in determining the present supremacy of the mammalian type. An unusual amount of plasticity and versatility is exhibited among mammals. For example, in size they vary from a certain field mouse scarcely more than an inch in bodily length, to whales which may attain a length of nearly 100 feet, or well over 1,000 inches (Fig. 49). Moreover, they are variously fitted for successful life in such diverse habitats as on the land (deer), in water (otter), in burrows (rabbit), under ground (mole), in the open sea (whale), in trees (squirrel), and in air (bat).

Some of the diagnostic characteristics of mammals are: (1) hair, at least in embryonic life; (2) sweat glands in the skin; (3)

a muscular diaphragm; (4) a larynx or voice box, at the upper end of the trachea; (5) two sets of differentiated teeth; (6) seven cervical vertebræ, except in the "manatee" and "two-toed sloth," each of which has six, and the "three-toed sloth," which has nine; (7) two occipital condyles, instead of one as in reptiles and birds; (8) marrow-bones; (9) red blood cells that lose their nuclei, except in the camels; (10) an elaborate prenatal life in the uterus of the mother, allowing for extended embryonic development in safety; (11) milk production to supply the first food of the young; and (12) obligatory postnatal care of the young by the mother, making possible the process of learning during a prolonged association with the parents.

The salvation of higher animals has depended upon the replacement of inherited instincts by the power and necessity of *learning anew in each generation how to live.* Inherited instincts make it possible for an animal to meet life only in a predetermined way, but learning anew in each generation opens up the possibility of alternatives of action, and an eventual development of intellectual life.

Living mammals may be arranged in twelve orders, which fall into three subclasses:—PROTOTHERIA, METATHERIA, and EUTHERIA.

1. Prototheria

The *Prototheria* (*proto*, first; *theria*, beast) comprise a single order, *Monotremata*, of which there are but three genera living today, namely, *Echidna*, *Pröechidna*, and *Ornithorhynchus*. They are curious, exceptional mammals that lay relatively large, yolk-laden eggs, from which the young are hatched instead of being born alive, in the usual mammalian fashion. *Ornithorhynchus* incubates its leathery-shelled eggs in a shallow nest of grasses, while *Echidna* forms a temporary pouch from a fold of the skin upon its belly, in which the newly laid egg is placed and incubated until hatched. In this portable nest the helpless young animal is kept through the precarious days of its early growth and fed upon a nutritious substitute for true milk, secreted by the mother from modified sweat glands. It is licked up from the wet hairs by

FIG. 50. — Young *Echidna*. (After Semon.)

the long tongue of the young *Echidna* (Fig. 50), since there are no nipples present. If there were nipples present the baby monotreme would not be able to suck, since its mouth is prolonged into a horny toothless beak, not at all fitted for the muscular operation of sucking, but which becomes useful later for poking into anthills after food.

Fig. 51.—The "duckbill," *Ornithorhynchus*, an Australian monotreme with webbed toes and a ducklike bill. (After Beddard.)

In *Ornithorhynchus* the beak is large and flattened, giving rise to the common name, "duckbill," by which this curious creature is known, a name all the more applicable because it lives much of the time in water, and has feet with webbed toes like those of a duck.

Ornithorhynchus is a native of South Australia and Tasmania (Fig. 51). *Echidna* is found in Australia, Tasmania, and New Guinea (Fig. 52), and *Pröechidna*, whose unusually long snout gives it "a ridiculous resemblance to a miniature elephant," is confined to New Guinea.

Fig. 52.—The spiny anteater, *Echidna*, a monotreme. (After Beddard.)

2. Metatheria

The *Metatheria* (*meta*, after; *theria*, beasts), or "marsupials," are primitive, or possibly degenerate mammals whose young, born prematurely in an extremely helpless condition, are carried about in a *permanent* brood pouch (marsupium), and are fed upon true milk. At first the young are unable to exercise the necessary muscular effort involved in sucking, and are securely attached in a passive way to the nipple by means of a sphincter-like mouth (Fig. 153), while the contraction of muscles across the breast of the mother expresses milk from her mammary glands down the throat of the helpless fetus. Later on as development advances the young marsupial draws its milk in orthodox style like other mammals.

Osborn, in *The Age of Mammals*, catalogs seventy-six genera of marsupials of which thirty-seven are extinct. The living ones, ex-

cepting the opossums of North, Central, and South America, and the marsupial shrew, *Cænolestes*, of Central America, are confined to the Australian region, while the extinct genera ranged over what

FIG. 53.—Marsupials. *A*, the "koala," or marsupial bear, *Phascolarctos*; *B*, "Tasmanian devil," a marsupial hyena, *Sarcophilus*; *C*, "wombat," a marsupial woodchuck, *Phascolomys*; *D*, marsupial mole, *Notoryctes*. (All after Beddard.) *E*, the "rock wallaby," *Petrogale*, a kangaroo. (After Vogt and Specht.) *F*, Virginia opossum, *Didelphys*. (From Stone and Cram, after Dugmore.) *G*, *Didelphys*, showing the young at the mouth of the pouch. (From Stone and Cram, after McCadden.)

is now Europe, as well as both Americas and Australasia. It is considered probable that the origin and spread of marsupials occurred before the ancient land bridge that joined Australia to South America had disappeared, and that those forms which became

isolated in Australia at that time were afterwards able merely to continue their handicapped existence, since they were not brought into competition with the true mammals that developed later on the other great continental areas.

It is a striking fact, moreover, that not only all the native mammals of Australia were marsupials, but that the Australian marsupials have become diversified into different types much in the same way that the true mammals have. Thus there are marsupial "bears," *Phascolarctos;* "wolves," *Thylacinus;* "hyenas," *Sarcophilus;* "cats," *Dasyurus;* "rabbits," *Thylacomys;* "jumping mice," *Antechinomys;* "woodchucks," *Phascolomys;* "moles," *Notoryctes;* "mice," *Sminthopis,* etc., as well as kangaroos and opossums. All of these animals are marsupials, occupying a great variety of habitats and showing a wide range of adaptations strikingly similar to those exhibited by true mammals elsewhere. Some of the marsupials mentioned above are represented in outline sketches in Fig. 53, A–G.

3. Eutheria

The *Eutheria* (*eu,* true; *theria,* beasts), including all the other mammals, are frequently termed "placentals," because they are all characterized by the presence of an embryonic organ, the *placenta,* which forms a living connection between the mother and offspring throughout the long preparatory life before birth.

FIG. 54.—Common mole, *Scalopus.* (After Schmid.)

Arranged according to the degree of specialization from the most generalized to the most aberrant, the orders of living placentals are:—INSECTIVORA, DERMAPTERA, CHIROPTERA, CARNIVORA, RODENTIA, EDENTATA, PRIMATES, UNGULATA, SIRENIA, CETACEA. A word of identification and comment about each of these ten orders of true mammals, with mention of a few representatives, is essential in completing a roll call of the vertebrates.

The *Insectivora* subsist largely upon insects, hence their name. They are mostly small, sharp-snouted animals, with leanings towards nocturnal or subterranean life, and include among other genera, the European hedgehog, *Erinaceus;* the common "tenrec"

of Madagascar, *Centetes;* the moles, of which the common mole, *Scalopus* (Fig. 54), and the star-nosed mole, *Condylura*, are American genera; and the shrews of various lands, *Sorex* and *Blarina* being North American representatives. Osborn names forty-five fossil, and thirty-four living genera of insectivores.

Fig. 55.—Flying lemur of Madagascar, *Galeopithecus*. (After Vogt and Specht.)

The *Dermaptera*, which are without fossil representation, are set aside into an independent order because of a single genus, *Galeopithecus* (Fig. 55), a "flying lemur" of the Malay region, that is an anatomical connecting link between insectivores and bats.

The *Chiroptera*, or bats (Fig. 56), are mammalian aviators which fly at twilight by means of enormously elongated webbed fingers. While the floppy flight of bats is by no means as sustained as the more powerful flight of birds, yet, aided by extremely responsive sense organs, these creatures are unsurpassed in avoiding obstacles and hawking insects in the crepuscular traffic of semi-darkness. The food of bats in general, and of North American bats in particular, consists practically of insects caught on the wing. In the Old World tropics the habit of eating fruit has developed in certain large bats, or "flying foxes," that live upon figs, guavas, and similar fruits. Another curious adaptation in the chiropteran type is presented by the blood-sucking vampires of Central and South America, that have a highly modified saclike stomach for the storage of blood which they gorge from some unwilling host.

Fig. 56.—An insectivorous bat, *Synotus*. (After Vogt and Specht.)

Representative bats are the common brown bat, *Myotis*, of cosmopolitan distribution; the flying fox, *Pteropus*, of southeast Asia and the East Indies; and the blood vampire, *Desmodus*, of Mexico and South America. Of sixty-three genera in Osborn's list only three are extinct.

The *Carnivora* are the alert, resourceful flesh eaters, represented by 73 living, and 113 extinct genera. The suborder *Fissipedia* is made up principally of land animals, while the suborder *Pin-*

FIG. 57.—Fissipede carnivores. *A*, wolf, *Canis lupus*. (After Beddard.) *B*, coyote, *Canis latrans*. (From Stone and Cram, after Dugmore.) *C*, red fox, *Vulpes fulvus*. (From Stone and Cram, after Dugmore.) *D*, raccoon, *Procyon*. (After Fuertes, in Nat. Geog. Mag.) *E*, polar bear, *Thalassarctos*. (From Stone and Cram, after Dugmore). *F*, mink, *Putorius*. (From Stone and Cram, after Speight.) *G*, civet cat of the Orient, *Viverra*. (After Beddard.) *H*, striped hyena, *Hyæna*. (After Schmid.)

nipedia comprises fish-eating carnivores that have become secondarily modified for aquatic life. As delegates to represent the fissipede carnivores, may be mentioned the following genera: *Canis*, dogs, wolves, and coyotes; *Vulpes*, red foxes; *Procyon*, raccoons; *Ursus* and *Thalassarctos*, bears; *Mustela*, martins and their allies; *Putorius*, the weasels and minks; *Taxidea*, badgers; *Mephitis*, skunks; *Viverra*, civets; *Herpestes*, mongooses; *Hyæna*, hyenas; *Felis*, cats, lions, and their kind; and *Cynælurus*, the "cheetah" of India, a cat without retractile claws (Fig. 57, A–H). Among the pinnipede carnivora (Fig. 58), some genera

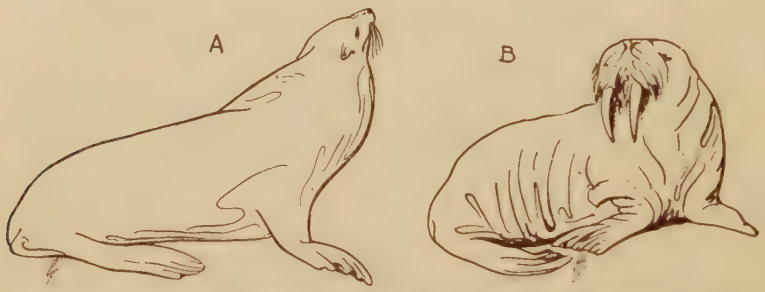


FIG. 58.—Pinnipede carnivores. *A*, California sea lion, *Zalophus*. (From Stone and Cram, after Dugmore.) *B*, Arctic walrus, *Odobænus*. (After Schmid.)

are *Otaria* and *Zalophus*, the sea lions; *Odobænus*, walruses; and *Phoca* and *Cystophora*, the seals.

The *Rodentia*, or gnawing animals, with 101 living and 61 fossil genera, are the most numerous of all living mammals, particularly as they make up in number of individuals what they lack in size. They are prevailingly plant eaters, and form an important link in nature's chain, since they hand on the sun's energy stored by green plants, to the carnivores which in turn devour them.

The rodentian bloc (Fig. 59), in the congress of mammals may be represented by the following genera: *Lepus*, rabbits and hares; *Sciurus*, squirrels; *Cynomys*, prairie dogs; *Sciuropterus*, flying squirrels; *Tanais*, chipmunks; *Castor*, beavers; *Perognathus*, pocket mice; *Geomys*, pocket gophers; *Mus*, rats and mice; *Myodes*, lemmings; *Microtus*, voles; *Fiber*, muskrats; *Zapus*, jumping mice; *Dipus*, jerboas; *Erethizon*, porcupines; *Histrix*, hedgehogs; *Cavia*, guinea pigs; *Peromyscus*, white-footed mice; and *Marmota*, woodchucks.

The *Edentates* (Fig. 60), are rather degenerate mammals, either

toothless, as the name signifies, or with very poor chalky teeth. Their home is in South America, for only three of the eighteen living genera are found elsewhere, although the anteaters, *Tamandua*, *Myrmecophaga*, and *Cyclopes*, extend as far north as Central

FIG. 59.—Representative rodents. *A*, squirrel, *Sciurus; B*, prairie dog, *Cynomys*. (Both from Stone and Cram, after Dugmore.) *C*, flying squirrel, *Sciuropterus*. (From Newman, after Lydekker.) *D*, beaver, *Castor*. (From Stone and Cram, after Dugmore.) *E*, muskrat, *Fiber*. (From Stone and Cram, after Carlin.) *F*, jumping jerboa, *Dipus*, of Europe. (After Beddard.) *G*, porcupine, *Erethizon*. (From Stone and Cram, after Dugmore.)

America and Mexico, and the nine-banded armadillo, *Tatusia*, reaches even Texas. Of the thirty-six genera of fossil edentates, two are from Europe and Africa, four from North America, three from both North and South America, and twenty-five exclusively

from South America. Thus it is evident that the center of distribution of this order has been South America. Indeed, the three genera of African edentates, that is, *Manis* and *Pholidotus*, "pangolins," and *Orycteropus*, the "aard-varks" of the Boers, are placed by Osborn, for geographical as well as anatomical reasons, in two separate orders by themselves. The "sloths," *Bradypus* (three-toed), and *Cholepus* (two-toed), are well named because of their sluggish habits. They are awkward, helpless creatures, clothed with coarse, gray hairs and equipped with long, hooklike claws which enable them to hang upside down in the branches of tropical trees, where they depend upon their resemblance to motionless masses of gray beard mosses for protection from their

FIG. 60.—Edentates. *A*, scaly anteater of Africa, *Manis*. (After Beddard.) *B*, ground hog, *Orycteropus*, the "aard-vark" of Africa. (After Schmid.) *C*, three-toed sloth, *Bradypus*, of South America. (After Schmid.) *D*, six-banded armadillo, *Dasypus*. (After Brehm.)

carnivorous foes. Of the armadillos, besides the nine-banded *Tatusia* already mentioned, there are the three-banded *Tolypeutes*, the six-banded *Dasypus*, and the eleven-banded *Xenurus*, all of which roll up in their scaly armor like "pill bugs" when danger threatens, and so present a hard nut for any predaceous enemy to crack.

The *Primates* (Fig. 61, A–G), including thirty-nine living genera of lemurs, monkeys, apes and man, while not so highly specialized in their entire bodily structure as the three orders yet to be mentioned, stand first in the vertebrate class with respect to brain development. Most of the twenty-three fossil genera of this order are lemurs, which no doubt dwelt in trees, as their modern representatives

of the Madagascar forests do to this day. Primates generally are largely arboreal in habit (Fig. 61), and tend to assume an upright

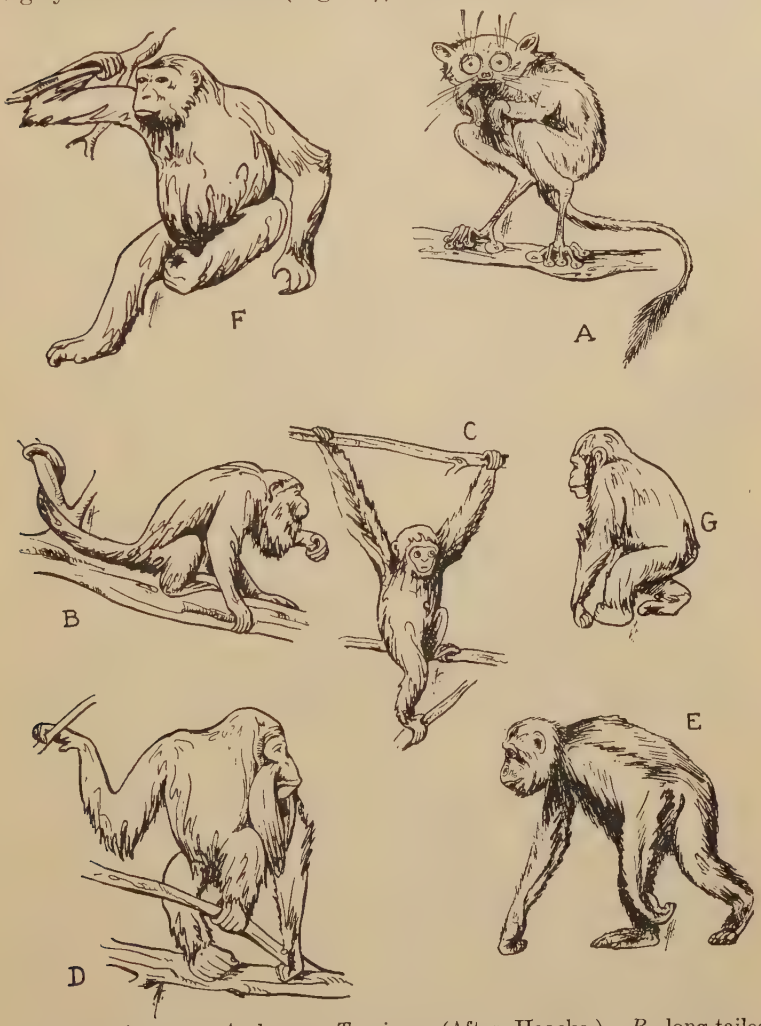


Fig. 61.—Primates. *A*, lemur, *Tarsius*. (After Haacke.) *B*, long-tailed monkey, *Alonatta; C*, gibbon, *Hylobates; D*, orang utan, *Simia*. (After Schmid.) *E*, gorilla, *Gorilla*. (After Beddard.) *F*, *Gorilla*. (After Schmid.) *G*, chimpanzee, *Anthropopithecus*. (After Schmid.)

posture that makes possible the development of a pair of handy hands. Organs of defense, like scales, claws, horns, and hoofs, are not needed by Primates, since wits take their place.

The platyrrhine, or broad-nosed, long-tailed monkeys of the New World are racially older and more primitive than the short-tailed, catarrhine monkeys of the Old World. *Hapale*, the little marmoset; *Ateles*, the spider monkey; *Mycetes* and *Alonatta*, the howlers; and *Cebus*, the Capuchin monkey, which made the hand organ famous, are samples of the former kind, while *Papio*, the mandrill; *Cynocephalus*, the solemn baboon; and *Macacus*, the lively macaque, which is so frequently seen serving time behind the bars in zoölogical gardens and menageries, are representatives of Old World types.

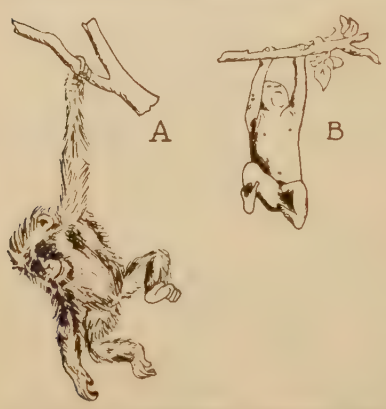


FIG. 62.—The arboreal habit of primates. *A*, a young chimpanzee, hanging to a branch. (After Leche.) *B*, a baby ten days old, which was able to hang from a support for ten minutes. Compare the attitude of the feet with that in *A*. (After a photograph by Romanes.)

There are four genera of living tailless apes, which are as far above the monkeys in the scale of intelligence as man is above the apes. They are the gibbon, *Hylobates*, of long arms and arboreal habit, from southeastern Asia and the East Indies; the orang utan, *Simia*, of Borneo and Sumatra; the powerful gorilla, *Gorilla*, and the chimpanzee, *Anthropopithecus*, the two latter both from Africa. The apes, particularly the chimpanzees, are capable of a considerable degree of education. They can be taught to wear clothing, dine at a table, ride a bicycle, smoke a pipe, expectorate with precision, and perform many other acts characteristically human.

Modern man, of whatever race or color, belongs zoölogically to a single genus and species, *Homo sapiens*, *L.*, although the name (wise man) is more appropriate for some human individuals than for others. Fossil man will be considered in a later chapter (page 98).

The *Ungulata* are the hoofed animals. For the most part they are large, rather stolid, plant-feeding creatures, most at ease when standing upon their highly specialized feet which are adapted for bearing continuous weight by being encased in shoelike hoofs. Unlike the soft-footed carnivores, which collapse into a reposeful, recumbent posture at every opportunity, only to spring into alert

activity upon the slightest provocation, the ungulates never sit down at all, and do not even lie down without considerable deliberation.

The seventy-three genera of ungulates include many kinds of great utility to man. They have, moreover, played a notable rôle in the past history of the world, as evidenced by the fact that 204 genera of fossil ungulates are known, many more than of any other order of mammals, although these numbers are no doubt due in part to the readiness with which they fossilize.

The living forms may be considered under four suborders:—ARTIODACTYLA, PERISSODACTYLA, PROBOSCIDEA, and HYRACOIDEA.

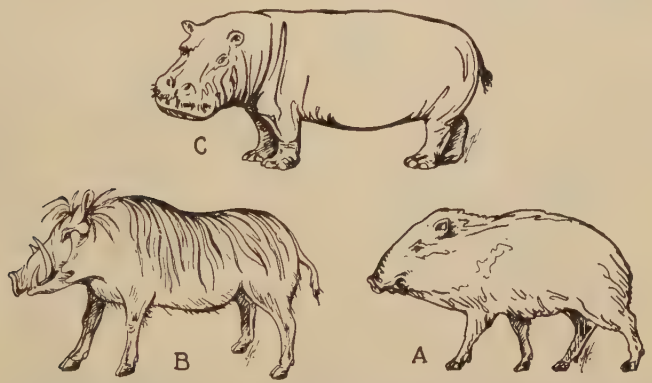


FIG. 63.—Non-ruminant artiodactyls. *A*, peccary of South America, *Pecari; B*, wart hog of Africa, *Phacochœrus; C*, *Hippopotamus* of Africa. (All after Beddard.)

The artiodactyl ungulates have an even number of toes on each foot. They may be grouped into those which swallow their food once for all, like the hogs and hippopotami, and those that are ruminant cudchewers, regurgitating hastily swallowed grass or herbage for a more thorough mastication later, at their leisure.

Examples of non-ruminant genera are *Sus*, the swine, natives of Europe which have followed man as his domesticated allies the world over; *Pecari*, the hoglike "peccaries" of South America; *Phacochœrus*, the wart hog of Africa; *Babirusa*, the wild boar of Celebes; and *Chœropsis* and *Hippopotamus*, the four-toed hippopotami of Africa (Fig. 63, A-C).

Ruminant artiodactyls are provided with defensive horns, either hollow and permanent, like those of a cow, or solid and

periodically shed and renewed, like the antlers of a stag. Representative ruminants are: camels and dromedaries, *Camelus*, the so-called "ships of the desert"; South American llamas, *Auchenia;*

FIG. 64.—Representative ruminants. *A*, camel, *Camelus bactrianus*. (After Beddard.) *B*, dromedary, *Camelus dromedarius*. (After Schmid.) *C*, llama of South America, *Auchenia*. (After Beddard.) *D*, chevrotain of India, *Tragulus*. (After Beddard.) *E*, giraffe, *Giraffa; F*, okapi, *Okapia*. (After Schmid.)

deerlike chevrotains of the Orient, *Tragulus;* towering giraffes of Africa, *Giraffa;* the curious, rare Congo okapi, *Okapia;* the musk deer of Indo-China, *Moschus;* true deer of various countries,

Cervus; reindeer of the Arctics, *Rangifer;* moose and elk, *Alces;* pronghorn antelope of the Rocky Mountains, *Antilocapra;* gazelle of Africa, *Gazella;* chamois of the Alps, *Rubricapra;* antelopes,

FIG. 65.—Horned ruminants. *A*, reindeer, *Rangifer.* (After Beddard.) *B*, arctic musk ox, *Ovibos.* (After Schmid.) *C*, American buffalo, *Bison; D*, moose, *Alces.* (After Beddard.) *E*, antelope, *Antilopa.* (After Schmid.) F, pronghorn antelope, *Antilocapra.* (From Stone and Cram, after Dugmore.)

Antilope; goats, *Capra;* sheep, *Ovis;* musk ox of Arctic regions, *Ovibos;* yak of Himalaya, *Pöephagus;* domestic cattle of all kinds, *Bos;* and the American bison, *Bison* (Fig. 64, A–F, and Fig. 65, A-F).

Perissodactyl ungulates are those with an odd number of toes on each foot (Fig. 66). The principal genus is *Equus*, which includes the horse and its allies, the ass and zebra. These animals have perhaps the most definitely traced pedigree of all mammals, since their record goes all the way back by successive links to a small five-toed ancestor which was about the size of a fox, and lived in Eocene times. Other perissodactyls are the tapirs of South

FIG. 66.—Perissodactyl ungulates. *A*, wild ass of Syria, *Equus onanger; B*, tapir of South America, *Tapirus; C*, two-horned rhinoceros of Africa, *Rhinoceros bicornis; D*, one-horned rhinoceros of India, *Rhinoceros indicus*. (All from Beddard.)

America, *Tapirus*, and the rhinoceroses, *Rhinoceros*, of Africa (two-horned) and of India (one-horned).

The *Proboscidea* are the elephants, largest of land mammals, which are so bulky that they are obliged to walk stiff-legged in order to support their tremendous weight (Fig. 67). The heavy head is sustained horizontally by a short, stout neck, and the rigidity brought about by this arrangement, as well as by the stiff uncompromising fore legs, is compensated by the development of a "trunk," which is the nose and upper lip together, enormously drawn out into a flexible, prehensile organ. Some proboscidians, as the mastodons and hairy mammoths of northern countries, became extinct in comparatively recent times geologically, while other less specialized ancestors, as *Dinotherium* of

Europe and Asia, and *Palæomastodon* of Egypt, are considerably more ancient. There are two genera of living proboscidians, *Elephas*, the Asiatic elephant, and *Loxodonta*, the African elephant.

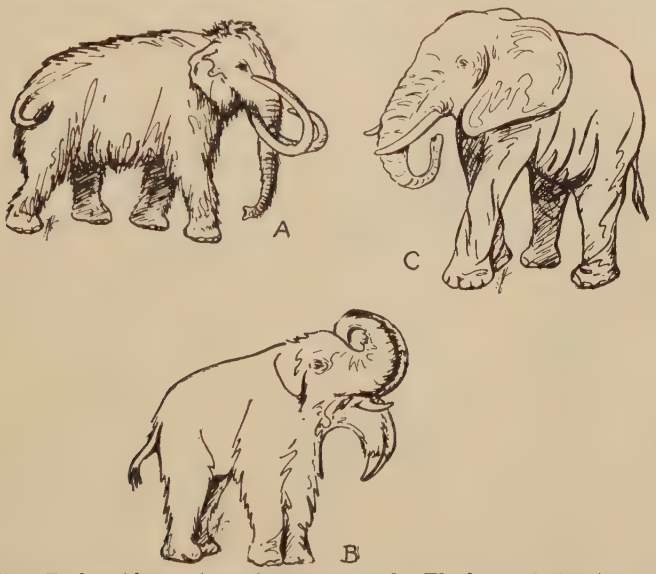


FIG. 67.—Proboscidea. *A*, extinct mammoth, *Elephas primigenius*. (After Schmid.) *B*, restoration of an extinct dinothere, *Dinotherium giganteum*. (After Abel.) *C*, African elephant, *Loxodonta*. (After Schmid.)

The *Hyracoidea*, or coneys, include two genera, *Dendrohyrax* (Fig. 68), of Africa, and *Hyrax* of Syria and Arabia. They are little cud-chewing animals resembling guinea pigs, with small hooflike tips to their toes, and, according to the Book of Proverbs, "are but a feeble folk, yet make they their homes in the rocks."

FIG. 68.—African coney, *Dendrohyrax*. (After Beddard.)

FIG. 69.—Atlantic sea cow or manatee, *Trichechus*. (From Stone and Cram, after Dugmore.)

The *Sirenia* are perhaps the animals that have furnished the slender basis of fact from which imaginative sailors from time immemorial have spun their tales of mythical mermaids and

sirens. A less romantic and more applicable common name for them is "sea cows," for they feed upon seaweeds, and, in spite of their abnormal form, show unmistakable relationship to vegetarian ungulates in many ways. They are large, clumsy water animals, having a broad snout covered with sparse, coarse bristles and an otherwise hairless skin. The anterior legs are modified into swimming flippers, while the hind legs are entirely absent.

Only two genera of this order are represented by living animals. They are distant from each other about as far as it is possible for them to be separated on the earth, since the "manatees," *Trichechus* (Fig. 69), inhabit the rivers of the northeastern coast of South America and beyond, as far north as the Everglades of Florida; while the "dugong," *Halicore* (Fig. 70), lives in the Red Sea and Indian Ocean.

FIG. 70.—Dugong, or Indian Ocean sea cow, *Halicore*. (After Schmid.)

Of the seven fossil genera, one, "Steller's sea cow," *Rhytina stelleri*, has been extinct only about one hundred and fifty years. It first became known in 1741, when Steller, a Russian whaler, was shipwrecked upon a group of small islands in Behring Sea. He and his crew were saved from starvation because they found there a rookery of these large sea cows upon which they fed until they were rescued. During the next twenty-five years Russian whalers, with human greed and stupidity, hunted these valuable food animals to extinction until Nordenskiöld, who visited the islands in 1768, reported that the last individual of the colony had been killed. They have never been found elsewhere.

The *Cetacea*, or whales and their allies, among which are to be found the largest known living animals, include the leviathans of the ocean. They have undergone profound specialization for marine existence, yet they present unmistakable hallmarks of true mammals, as, for instance, breathing air by means of lungs and feeding the young upon milk. While in the act of nursing, which is obviously accomplished under difficulties, the young whale presents a curious resemblance to a small tug attached to the side of an ocean liner (Fig. 145). By reason of their warm-

bloodedness and a thick blanket of heat-retaining blubber under the skin, these gigantic animals are able to pursue their activities even in arctic waters.

Whales may be grouped into two subclasses:—ODONTOCETI, or toothed whales, which feed primarily upon fishes; and MYSTACOCETI, or whalebone whales, which, by means of a peculiar

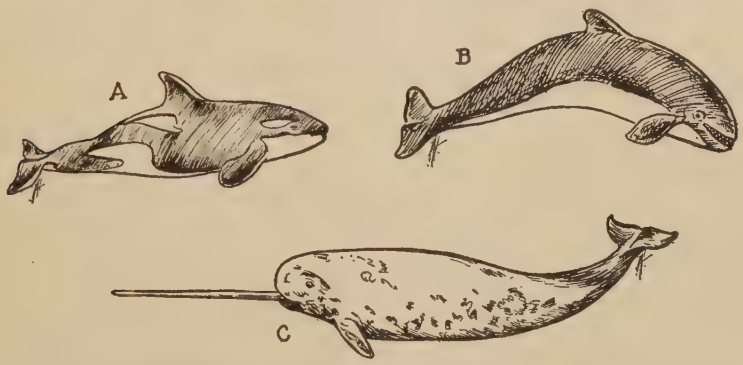


FIG. 71.—Toothed whales, or ODONTOCETI. *A*, "killer," *Orca*. (After True.). *B*, porpoise, *Phocæna; C*, narwhal, *Monodon*. (After Schmid.)

brushlike device of "whalebone" in the cavernous mouth cavity, strain out and swallow countless myriads of microscopic ocean inhabitants, that constitute for them a nutritious sea soup of unlimited supply.

The toothed whales (Fig. 71) are usually not of extraordinary size and frequently forage about in their watery hunting grounds in schools. Some of them are the dolphin, *Delphinus;* porpoise

FIG. 72.—Right whale, *Balæna*. (After Schmid.)

Phocæna; grampus, *Grampus;* "blackfish," *Globiocephalus;* killer, *Orca;* narwhal, *Monodon*, with a single enormous twisted tooth, projecting horizontally like a pikestaff; the sperm whale, *Physeter;* and the bottle-nosed whale, *Hyperoödon*. The last two attain considerable size.

The giants, however, are the whalebone whales, of which the

gray whale, *Rachianectes;* the rorqual, *Balænoptera;* the humpbacked whale, *Megaptera;* and the right whale, *Balæna* (Fig. 72), are examples.

There are nine genera of fossil cetaceans, and twenty-seven genera of living ones, some of which are becoming scarce because they have been so relentlessly hunted by man.

CHAPTER III

THE DISTRIBUTION OF ANIMALS IN SPACE (CHOROLOGY)

I. THE POINT OF VIEW

An observant traveler as he goes from home in any direction gradually leaves behind a familiar world of animals and plants, and if his travels are sufficiently extensive, he arrives in a land of strange organisms perhaps quite unlike those he already knows. He discovers that no one kind of animal is to be found everywhere, but that each kind has its own home territory beyond which it does not ordinarily venture.

In imagination he might map out upon the globe the home patch, with all its irregular boundaries, which each of the 600,000 or more species of living animals occupies. Of course it would form an exceedingly complex patchwork, because the areas thus delimited would be very unequal in size and shape, and would overlap each other in a great variety of ways like a gigantic palimpsest. A diagram to express this idea, in which the areas of only six instead of 600,000 species are involved, is shown in Fig. 73.

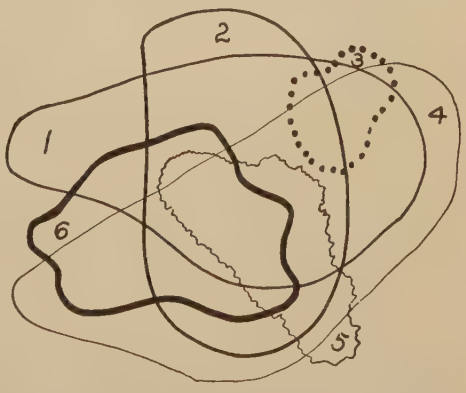


FIG. 73.—Hypothetical limits of the distribution of six different species of animals, arranged in superimposed areas.

Such a picture, moreover, if truly represented, would be a *motion* picture, presenting constant change like a kaleidoscope, for the frontiers established by living things can never remain constant. It is well known that animals in the past actually occupied territory from which they are absent today, and that

the contrary is equally true. Evidence from fossils, for example, shows that tropical parrots and arctic reindeer were once natives of what is now temperate France, that elephants formerly roamed over the United States, and that antarctic albatrosses flew over England.

The *locality* where any species of animal is found is just as much a diagnostic characteristic of the kind of animal in question as its peculiarities of structure or behavior. It follows that not only fossils but any kind of living animals lose much of their value for the scientist who would study them, if their home place is unknown.

II. HABITATS

The immediate surroundings in which any animal is at home constitute its *habitat*. Thus, animals are said in general to occupy either a land or a water habitat. Some of the more specific terms applied to habitats are desert, forest, mountain, subterranean, marsh, pelagic, abyssal, pond, marine, and fluviatile. This list of descriptive terms, applicable to local conditions, may be almost indefinitely extended, according to the minuteness desired in the description. The arrangement of these various kinds of habitats over the surface of the globe determines to a large extent the distribution of living forms. It is obvious, for instance, that arboreal animals are not to be expected in the open ocean, nor fishes in waterless deserts.

Animals found living successfully in any habitat must be measurably adapted for life there, although there are many cases in nature of imperfect adaptation where a square peg is attempting to fill a round hole. The usual result in such a misfit is that the peg either goes further until it finds its proper hole, or gradually changes to fit the hole it is in. Both hole and peg are changeable things, but the hole does not often change to fit the peg, for the initiative is not with the hole but with the peg.

Not all habitats, moreover, are occupied by animals and plants adapted to live in them. The popular idea that climate, for example, determines the distribution of organisms, is largely erroneous. There are no grizzly bears in Switzerland, no birds-of-paradise in California, nor "snakes in Ireland," although the climate in each case is suitable for the absentees. The equatorial forests of Africa and South America have practically the same

climate, yet the former region is characterized by elephants, apes, leopards, and guinea fowls, while the latter has none of these animals, but does support tapirs, long-tailed monkeys, jaguars, and toucans, which are never found in Africa. What then are the factors that determine the present distribution of animals and plants? Why are animals located where they are? For answers to such questions as these we must turn to the sciences of ECOLOGY and CHOROLOGY.

III. THE SCOPE OF CHOROLOGY

The science of *Ecology* (*oikos*, home; *logos*, discourse) deals with the intimate arrangement and behavior of organisms within their respective habitats. It is the province of the more inclusive science of *Chorology* (*choros*, place; *logos*, discourse) to determine the general distribution of animals and plants over the earth, and to formulate the laws which determine their location in nature.

So long as mankind was satisfied with the naïve supposition that the earth had been arbitrarily populated by independent acts of special creation, much as a person might arrange chessmen upon a board, there was no sense or object in the science of chorology. There was nothing to explain. Leopards, for example, were in Africa, and jaguars in South America, because they were placed there in the beginning. The two kinds of animals were entirely independent and without any relation to each other. When, however, the conception, culminating with Darwin, that all organisms are more or less related to each other, and that every species arose in the course of time by modification from some other species, then the *manner of distribution* over the earth became full of significance and seriously challenged the attention of thinking people.

IV. THE LAWS OF DISTRIBUTION

Jordan and Kellogg [1] have formulated three "laws" governing the distribution of animals which, with some abbreviation, may be stated as follows: *Every species is found everywhere that conditions are suitable, unless* (1) it was unable to get there; (2) having "got there" it was unable to stay; or (3) having "got there" it became modified into another species. It will be profitable to consider these "laws" briefly. First, it is not *suitability* of the

[1] *Animal Life.* D. Appleton & Co.

habitat that determines the presence of an inhabitant, but *accessibility* from the place of the inhabitant's origin. For instance, there are no hummingbirds in Africa, while there are over 450 species in South and Central America, not because Africa itself is unfavorable to hummingbird occupation, but because these tiny, fairylike creatures have never been able to cross the wide oceans separating their ancestral American home from far away Africa.

Second, there are many instances of animals and plants that have succeeded in invading new territory, but have been unable to hold their own there. Several years ago the U. S. Government introduced a herd of camels into the semi-arid region of the Southwest, and allowed them to run wild in the hope that they would multiply, spread, and eventually form a valuable addition to a region inhospitable to most large animals. The environment was very like that from which the camels came and the experiment might have proved successful but for the unfortunate fact that local cowboys, with little regard for consequences, had so much sport periodically rounding them up and putting them through their paces, that the strange incongruous beasts were literally worried to death.

Third, successful pioneers may win out in occupying new territory at the expense of their own specific individuality. They are adaptable round pegs thrown into new habitats of square holes, that nevertheless remain and eventually square themselves to fit the new holes. A classical illustration of cases of this kind is cited by Darwin,[1] of animals upon the Galapagos Islands off the northwestern coast of South America. Of twenty-six species of land birds found upon these islands, twenty-three species were similar to, but still specifically different from those inhabiting continental land a few hundred miles away. The interpretation given by Darwin is that when the Galapagos group was separated from the mainland in recent geological times, a new habitat was formed in which various individuals of continental species were isolated. In the course of time, twenty-three species of these birds came to assume an alias, because, under the molding influence of isolation, they had grown to be sufficiently different from their mainland ancestors and cousins to rank as entirely different species. These facts so impressed Darwin that he began

[1] *Origin of Species.*

to think about the *origin of species*, with the fortunate result that subsequently a great many other people were induced to think about the same subject.

To these three laws of distribution may be added a fourth, namely: *Each species originated historically from some preceding species at some definite place, and its present distribution is the result of two opposing factors,* EXPANSION *and* REPRESSION.

V. MALTHUS' LAW OF OVER-PRODUCTION

It would be as impossible for an unrestrained gas to remain in one place, as for any species of animals to forego the attempt to occupy unoccupied territory to which it has access. The reason for this is the enormous expansive possibilities inherent in the reproductive processes of all organisms, a condition formulated by Malthus in his "Law of Over-production." For example, when a single cod produces 9,000,000 eggs, it is obvious that infant mortality must come to the rescue, or within a few generations every available inch of space in the ocean would be preëmpted by codfish.

Even slow-breeding animals like elephants, which produce perhaps six young in a lifetime of a hundred years, would require, according to Darwin, only about 750 years to produce from a single pair, nearly 19,000,000 elephants. Allowing twenty feet for each elephant, this would make a continuous parade, which would have delighted Barnum's heart, reaching one and a half times around the world at the equator. Elephants and codfish, however, do not multiply out of all bounds as the above figures suggest, for the expansive forces of reproduction are kept in control by opposing repressive factors which, year in and year out, maintain a balance in nature.

VI. FACTORS INDUCING EXPANSION

1. The Food Problem

Somewhere in one of his delightful essays, Dr. Crothers presents the illuminating statement that "the haps and mishaps of the hungry make up natural history." There is no doubt that the insistent need for food, as expressed by hunger, is a mainspring of animal activity, which, like a centrifugal force, compels animals to go forth in quest of what they may devour. Even among higher animals, which exercise parental care, there comes a time when the

young may no longer share food with their parents but must seek fresh pastures. It would be disastrous, to illustrate with a botanical case, if the acorns produced by an oak tree all remained to grow within the parental circle.

Not only is there competition for food and place among animals and plants of a kind, but there is severe rivalry between different kinds of creatures for the same food supply. The miscellaneous company which at any time sits at Mother Nature's table, does not always, or even often, observe the table manners of polite society, so that there is every inducement to go elsewhere.

2. Change of Habitat

Another general factor that causes organisms to spread, is change in habitat. Such a change may be transient, like the drying up of ditches and streams which affects aquatic organisms, or it may be permanent, like deforestation by man which renders arboreal animals homeless. It may be sudden and catastrophic, like a prairie fire, or a flood, forcing all sorts of animals to flee for their lives; it may be gradual like the change of seasons, when winter succeeds summer; or it may be so very slow that it extends over generations of time, like the relentless dawn of a glacial period.

In all cases, however, when an environment becomes unfavorable, there are at least four alternatives open to the inhabitants: (1) the organisms may simply succumb to the change in environment, completing their normal life cycles before the unfavorable conditions befall, as in the case of annual plants and most insects; (2) they may retire from active life and mark time while the unfavorable conditions last, like hibernating or encysting animals, and trees that shed their leaves in winter; (3) they may remain plastic enough to change themselves as the environment changes, thus keeping pace by adaptation to new conditions; or (4) they may forsake unlivable surroundings and seek a more favorable place to carry on, like migrating birds and emigrants of all kinds. This latter alternative of migration brought about by change in habitat, plays an important rôle in the expansive distribution of animals and plants.

VII. MEANS OF DISPERSAL

The ways and means, direct and indirect, that are employed by organisms for dispersal, furnish a fascinating chapter in natural

history. Only a few of the most common agencies may be mentioned here.

Among plants the *wind* is an important agent. In many instances seeds are rigged with ballooning or parachuting devices, or are so light as to be easily borne some distance upon currents of air. The tiny dustlike seeds of certain orchids, for instance, have been known to float in air from Holland across the North Sea, while the molds everywhere testify to the efficiency of air movements, however slight, in scattering the spores of these ubiquitous organisms. Over sixty species of North American birds have been reported, which have reached Europe and become established there by being borne out of their migratory routes, and insects which take wing, like grasshoppers for example, are frequently assisted in their widespread movements by the wind. It has been observed that mosquitoes of the Hackensack marshes in New Jersey are aided in their travels by the suction-like draft of air caused by the swift passage of railway trains through their populous habitat.

Water furnishes another highway for travel. The uneasy tides keep the congested inhabitants of the seashore constantly stirred up, while moving streams and ocean currents act continually as agents in the involuntary transfer of all sorts of organisms from one place to another.

Even floating *icebergs* are the precarious rafts upon which arctic animals frequently are borne some distance into new regions.

Animals themselves assist each other in dispersal in a multitude of ways. Parasites naturally go wherever their hosts go, and so are introduced into the society of new hosts. The larval "glochidia" of certain sluggish fresh-water clams of the genus *Unio* fasten themselves to the gills of swiftly moving fishes, thus stealing a ride to some distant point in the stream where they detach themselves and set up their semi-stationary housekeeping in a new place. Animals are particularly conspicuous agents in scattering the seeds of plants. "Sticktights" and burrs of all sorts are makeshifts on the part of plants to secure transportation by attachment to passing animals. Seeds too of various kinds are buried in attractive fruits with the result that they may be eaten by animals and so deposited in some new locality after passing unscathed through the digestive tube of the traveling animal. The mistletoe, which grows parasitically attached to branches of trees,

presents an extreme case of distribution through animal agency. Doves eat the mistletoe seeds which are encased in alluring sticky berries. Frequently it happens, much as when a small boy emerges from a jam closet, that the remains of the feast adhere around the margin of the mouth, and the dove flies away to another tree where it performs its toilet by wiping its sticky beak upon a branch. Thus a mistletoe seed may be wiped off and stuck to a branch in the exact situation favorable for the growth of a new plant in a new place.

Of all animals, however, *man* has probably done more than any other in furthering the spread of organisms. In many instances this has been done intelligently and to the ultimate benefit of man himself, as in the case of cultivated plants and domesticated animals. The landscape has been modified almost everywhere by the transforming hand of man. Crops of various kinds dot the globe where wilderness once flourished, while introduced flocks and herds roam in safety over territory which was once the battle-ground of native wild animals.

Frequently man has made serious mistakes, from the human standpoint, in meddling with the balance of nature. The introduction of that over-successful "avian rat," the English sparrow, into the society of American birds has been many times regretted, both by man and by the birds with which it comes into competition. The bloodthirsty mongoose, which was brought to Jamaica, and also to Hawaii, to kill rats in sugar cane fields, not only proved to be an efficient rat-killer, but went further and destroyed other animals, particularly chickens, so that poultry raising has been seriously interfered with, and now a price has been set on every mongoose's head. Several years ago a gentleman in Medford, Massachusetts, who conceived the idea that some more hardy insect than the silkworm might be found to spin silk, and at the same time feed upon less restricted food than the leaves of the mulberry tree, brought back from Europe a few gipsy moths, *Porthetria dispar*, to experiment upon. The box in which they were contained, the story goes, was accidentally knocked out of an open window and some of the moths escaped, but for the time the incident was forgotten. This was in 1869. By 1889 the descendants of these accidental pioneers had prospered to such an extent that the people around Medford became alarmed. "In that summer the numbers were so enormous that the trees were completely

stripped of their leaves, the crawling caterpillars covered the sidewalks, the trunks of the shade trees, the fences, and the sides of the houses, getting into the food and into the beds." A town meeting was held and $300 appropriated to fight the pest. This was a mere beginning, for since that time the State of Massachu-

Fig. 74.—Map of the New England States, showing the spread of the gipsy moth, *Porthetria dispar*. In 1900, twenty years after its introduction near Boston, it had spread over the area marked in black. The cross-hatched lines indicate its distribution in 1905, and the slanting lines its range in 1918. (After Brues.)

setts, as well as adjoining States and the Federal Government have repeatedly taken a hand in attempting the extermination or control of the gipsy moth. Dr. Lutz, writing in 1920 [1] says: "Millions of dollars have been spent in an effort, so far unsuccessful, to free us from the invader, and the most that has been done has been to confine it to New England." (See map above, Fig. 74.)

[1] Lutz, *Field Book of Insects*, G. P. Putnam's Sons, 1921.

The white cabbage butterfly, *Pieris rapæ*, first came to America from Holland in a sloop-load of wormy cabbages landed at Quebec in 1861. Twenty years later it had colonized America on the Atlantic Coast from Hudson Bay to Florida. In 1886 it had arrived at Denver, and in 1900 had reached the Pacific Coast, having accomplished the conquest of the entire United States in less than thirty years.

"Shipworms," *Teredo*, on the outside, and rats on the inside of the hulls of vessels, have spread themselves the world over wherever shipping has gone, and in 1827 mosquitoes, traveling as "wigglers" in the bilge-water of a sailing vessel carrying missionaries, arrived in the Hawaiian Islands. Both missionaries and mosquitoes have prospered since then and made the Islands their own.

Several years ago a marble statue, made by the sculptor Thorwaldsen in Italy, was set up in Copenhagen. As an accidental result twenty-five species of Italian weeds, the seeds of which were in the straw packing of the statue, are said to have made their appearance in the immediate vicinity. Similar instances could be indefinitely multiplied of the effects of the interference of meddlesome man with the natural arrangement of organisms in space.

VIII. FACTORS OF REPRESSION

Among the representative factors which hinder world conquest on the part of any single species of animals or plants, are: (1) inadequate means of dispersal; (2) non-adaptability to new conditions; and (3) barriers of various kinds.

1. Inadequate Means of Dispersal

The difficulties of "getting there" are not especially apparent in the case of freely moving animals like birds and insects, but they become very real and serious for many organisms whose structure is not particularly adapted to locomotion over considerable distances.

It has been experimentally determined [1] that a certain kind of flatworm, *Planaria gonocephala*, gliding in water by means of cilia along a path of mucus which it must first secrete and lay down upon some suitable substrate wherever it goes, travels at

[1] Walter, *The Reactions of Planarians to Light*, Jour. Exp. Zoöl. vol. V., 1907.

the rate of about 0.65mm. per second. Under the most favorable circumstances it would require about a month of strenuous, uninterrupted travel, day and night, on the part of such a flatworm to go a mile, which is not a very large unit of distance compared with the size of the earth. Probably no one flatworm either has, or can within its lifetime, get energy enough for so stupendous a journey, and even if it did acquire the requisite energy, and had adequate locomotor machinery for its use, it is entirely unlikely that it would ever devote itself to the consecutive effort necessary to go a mile, in a month or a lifetime. What is in general true of the flatworm applies to all sorts of animals which are poor travelers, yet the race is by no means always to the swift. The story of the tortoise and the hare finds plenty of parallels in actual happenings in nature. In 1841 when Gould, with his searching eye for molluscs of all kinds, wrote *A Report on the Invertebrate Animals of Massachusetts*, he made no mention of *Littorina litorea*, a small familiar periwinkle, that feeds upon the seaweeds along the seashore. In 1855 Morse found, in the Bay of Chaleur at the mouth of the St. Lawrence River, a few of these animals which had in some way been accidentally brought there from their original home in Europe. In 1875 Verrill reported two from Woods Hole, Mass., several hundred miles to the southward, and in 1880 Smith found the first one noted as far south as New Haven, Conn. At present this species of snails is one of the commonest along the Atlantic coast, in spite of the fact that individually it is not a facile wanderer. Its traveling ability was once tested by the writer who marked for identification 1,000 shells of *Littorina* living along a little strip of beach at Woods Hole. After a lapse of three weeks 567 of the marked snails were found still in the same restricted locality.

2. Non-Adaptability to New Conditions

The non-adaptability of organisms to new habitats which they may have invaded, is doubtless much greater than appears on the surface, and surely acts as a deterrent to the spread of organisms. Successful invaders that gain a new foothold and retain it, catch the eye and claim attention, while unsuccessful ones which reach the promised land but are unable to establish themselves there, escape attention and pass unnoticed.

Many plants which thrive under cultivation, like Indian corn

or maize, appear to be unable to maintain themselves in nature when they chance to run wild. The yellow-fever mosquito, *Stegomyia fasciata*, fortunately cannot succeed north of a certain dead line, although no doubt it has repeatedly crossed this invisible limit. The English ivy also, that clothes the walls of southern buildings in luxuriance, fails to grow well in more northern latitudes, although repeatedly planted and nurtured there.

3. Barriers

Barriers which check or stop organisms on all sides are at least three in kind:—PHYSICAL, GEOGRAPHICAL, and BIOLOGICAL.

Temperature is a widespread physical barrier. The exclusion of "cold-blooded" animals, such as amphibians and reptiles, from participation in the colonization of lands of prevailingly

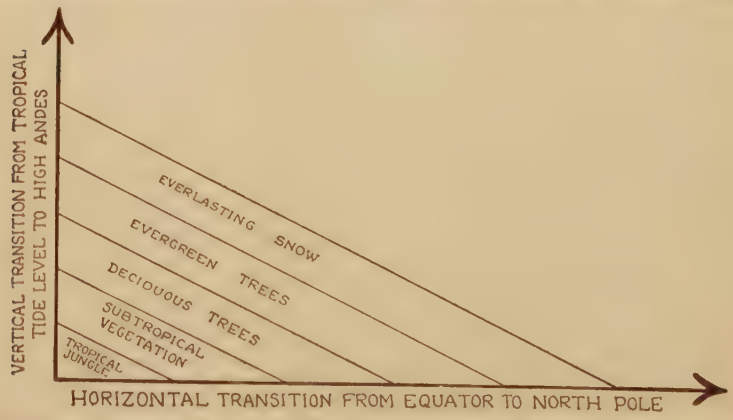


FIG. 75.—Diagram of the general parallel sequence of organisms in altitude and longitude.

low temperatures, is quite evident. In general, temperature zones extend not only in latitude, north and south from the equator, but also in altitude in a parallel succession from tropical sea level to high mountain peaks (Fig. 75).

In ocean depths *pressure* acts as a barrier that stratifies the inhabitants living therein within certain limits to which they have become specifically adapted. Deep-sea fishes cannot pass freely from abysses to surface waters, nor can pelagic forms sink far below and survive. Similarly there is an upper altitude limit in the air beyond which flying birds cannot rise.

Humidity sets up a barrier which according to its degree is largely impassable to exploring organisms that are dependent upon a certain optimum of water; and *light* is a physical barrier that halts the traffic of nocturnal darkness-lovers, although it usually has more of an ecological than chorological bearing.

Geographical barriers are such features of the earth's surface as oceans, land masses, rivers, mountains, waterfalls, deserts, forests, and the like. What is a barrier to one organism, however, may be a highway to another. Thus, a desert would form an impassable barrier to a squirrel but not to a camel, while a forest in which a squirrel would revel, would prove an effectual barrier to a camel.

Biological barriers are bound up, in the first place, with the eternal food problem, since the absence of food of a particular kind in a region prevents the advance of invading animals, while poverty of soil discourages occupation by plants dependent upon the missing constituents. Secondly, biological barriers are often created by the presence of other animals, by habit predaceous or parasitic, which forbid advance in certain directions. The "tsetse fly," *Glossinia*, that never goes far from the river bottoms in certain parts of tropical Africa, transmits a fatal blood parasite to cattle that approach within its range, thus debarring them from successful maintenance in these fertile areas. Thirdly, the greatest biological barrier of all is man, since he is able to control the forces of nature far more than any of his animal allies.

It should be pointed out that preventive barriers to the spread of animals may exist within the animals themselves in the form of scanty wits or lack of initiative which cause failure to enter in, even though the door of opportunity swings wide open.

If the factors of expansion and repression were equal in all directions the area occupied by each species would be a perfect circle, but such a case is unknown. The irregular shapes and boundaries of the claims actually staked out in nature by various organisms, proclaim the complex interaction of the fundamental opposing forces that determine distribution.

IX. CLASSIFICATION OF LIFE REALMS

An attempt has been made by chorologists to divide the land-masses of the world into *life realms*, according to the distribution of animals and plants. Such life realms in no way neces-

sarily coincide with the familiar political boundaries that separate nations from each other, for they are much more indefinite in their limits. Furthermore, it is evident that such life realms must vary according to the kind of animal or plant inhabitants selected to serve as their determinants.

Perhaps the first serious attempt thus to divide the earth into zoölogical realms, was made in 1851 by Sclater, who based his

NUMBER OF MAMMALIAN FAMILIES REPRESENTED IN EACH OF WALLACE'S SUBREGIONS

Families	Genera	Species	Orders	Region	Neotropical				Nearctic				Palæarctic				Ethiopian				Oriental				Australian			
				Subregion	1 Brazilian	2 Chilean	3 Mexican	4 Antillean	1 Californian	2 Rocky Mountain	3 Alleghenian	4 Canadian	1 European	2 Mediterranean	3 Siberian	4 Manchurian	1 East African	2 West African	3 South African	4 Malagasy	1 Indian	2 Ceylonese	3 Indo Chinese	4 Indo-Malayan	1 Austro-Malayan	2 Australian	3 Polynesian	4 New Zealand
2	2	3	Monotremata																					2		
7	36	149	Marsupialia		1	1	1		1		1												4	6		
8	26	134	Insectivora				1	1	2	2	2	2	3	4	3	3	2	2	4	1	2	3	3	4				
1	1	1	Dermaptera																	1								
5	79	445	Chiroptera		3	3	3	2	3	1	1	1	2	3	2	3	4	4	4	4	4	4	4	4	3	3	2	2
13	67	372	Carnivora		6	4	4		7	5	5	8	6	7	6	6	5	5	7	2	6	5	6	5	1	2	2	
16	99	779	Rodentia		5	7	5	3	8	7	7	8	6	8	8	5	9	6	8	1	5	4	5	4		1		
5	14	44	Edentata		2	3	3										2	1	2		1	1	1	1				
8	38	274	Primates			2	1						1	2	1	3	2	4	2	2	2	2	3	4	1			
10	59	275	Ungulata		2	3	3		2	3	2	2	3	6	5	3	8	8	8	1	5	5	6	7	3			
1	3	5	Sirenia			1		1					1		1		1	1			1	1		1	1			
6	53	155	Cetacea																									
82	467	2636			19	24	21	7	23	18	18	21	22	30	26	23	33	31	35	12	26	25	28	30	13	14	4	2

conclusions upon the distribution of birds. There are, however, some very apparent objections to utilizing such vagrant, barrier-defying creatures as birds for this purpose. Accordingly, in 1876 Alfred Russell Wallace, who if not the father of animal chorology must at least be reckoned as one of the founders of the science, divided the surface of the earth into zoölogical regions, based

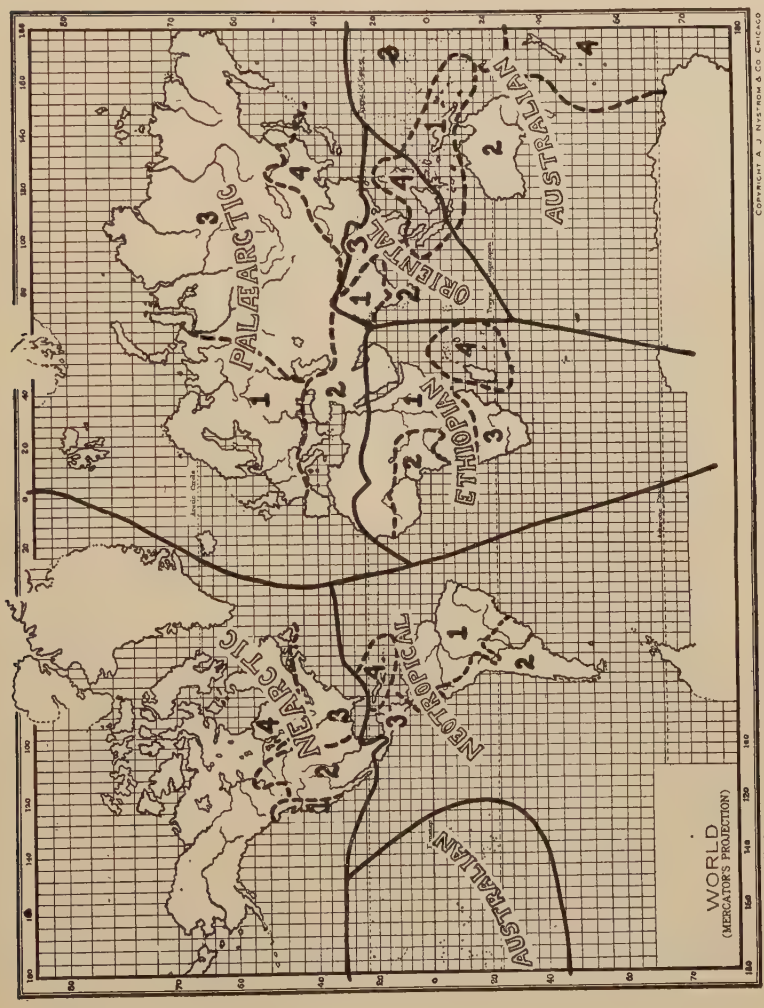


FIG. 76.—Mercator map of the world, divided into zoölogical regions and sub-regions. (According to Wallace.) (Compare with Table on page 84.)

chiefly upon the distribution of mammals. Reptiles, amphibians, fresh-water fishes, insects, and spiders have each in turn been used as the foundation for zoölogical map-making, as well as various combinations of animals, but no doubt mammals present the most advantages for this purpose. The reason for this lies in the fact that, although warm-blooded and thus capable of occupying a great range of habitats, mammals are the most recently evolved large group of animals on the earth, and have not had as much time as other types of animals to radiate from their centers of origin, with consequent confusion as to which species are native (*endemic*), and which introduced.

Wallace's classification consists of six large regions, each of which is divided into four subregions (as indicated in the table on page 84).

This table shows the number of different *families of mammals* represented in each of the twenty-four subregions, and is compiled from data collected by Wallace in his book upon *Distribution of Animals*. It will be seen from this table that bats (*Chiroptera*) are most generally represented, there being no subregion that does not have at least one of the five families of bats within its borders, while whales (*Cetacea*) do not appear at all, because they are not definitely associated with any land masses. The richest subregion, so far as number of mammalian families goes, is the *South African*, although the *East African*, *West African*, *Indo-Malayan*, and *Mediterranean* are likewise conspicuously populous. The poorest is the *New Zealand* subdivision, which can boast of no native mammals with the exception of two families of bats.

The Mercator map of the world (Fig. 76) shows roughly the extent of each of Wallace's regions and subregions.

CHAPTER IV

THE DISTRIBUTION OF ANIMALS IN TIME (PALÆONTOLOGY)

I. VANISHING SPECIES

It is quite as essential to an intelligent understanding of the organisms living upon the earth today, to have some vision of the long pageant of preliminary life in the past, as it is for a wise statesman to be well versed in the history of events leading up to the present state of affairs in which his immediate problems lie. *Species* of animals and plants, like individuals, pass through successive stages that resemble the phases of a single life. Expanding childhood, vigorous youth, sustained maturity, and decrepit old age succeed each other only to end inevitably in death or extinction. Sometimes a species, like an individual, may complete its life without leaving any issue behind, but oftener, in the long course of its existence, it somehow gives rise to species different from itself, a process which has brought about the infinite diversity of living forms that connect *monad* with *man*.

Certain conservative kinds of organisms, well adapted to their niches in nature, persist, retaining their characteristics without significant evolutionary advance for unthinkably long periods of time, while other species, exhibiting a wider range of variability, live a faster, more diversified life and advance more rapidly along the transforming highway of evolution, only to meet extinction sooner. The brachiopods, *Lingula* and *Terebratula*, for example, the modern living representatives of which are hardly to be distinguished from remote fossil ancestors found buried in the most ancient sedimentary rocks, are instances of conservative species that have shown almost no progress, while *Trilobites*, *Ammonites*, *Pterosaurs*, and *Dinosaurs* are large representative groups of more ambitious animals, of astonishing diversity of form and detail, which have long since paid the death penalty for their high degree of specialization.

Examples of all stages in the process of coming to an end on the part of a species may be cited. For instance, many kinds of

birds, like the heath hen, upland plover, snowy egret, and wood duck, are probably marked for extinction in the near future. This is not simply because they are being crowded off the earth by dominant man, but because they are in the biological blind alley of over-specialization with a corresponding lack of ability to adapt themselves to changing conditions, and are consequently nearing the end of their organic resources. In fact, birds, taken as a group, are so highly specialized that they have no evolutionary escape, since that is possible only in generalized types having capacity for further adaptation.

People now living remember the hordes of passenger pigeons that formerly darkened the skies, but the last individual of this species died in captivity only a few years ago, while the passing of the "dodo," the great auk, and Steller's sea cow are matters of recently recorded history. The mammoth, moa, sabre-toothed tiger, and woolly rhinoceros came to their end just before the beginnings of human history, and back of these recent antiquities stretches a long interminable line of various species whose chapter of existence closed so long ago that our ordinary measures of time entirely fail to express the fact adequately.

There is no doubt that living species number but a small fraction as compared with vanished ones formerly peopling the globe, whose race has long since been run. The dawn of life is unknown, for the oldest sedimentary rocks in which the first known evidences of life appear, yield a wide variety of forms, such as sponges, corals, jellyfishes, echinoderms, worms, brachiopods, molluses, and trilobites. This means that the great Canterbury Pilgrimage of organisms had already been traveling for some time along the evolutionary road, before we catch our first glimpse of the pageant.

II. FOSSILS

The ancient history of animals and plants forms the science of PALÆONTOLOGY. Fossils make up the alphabet in which the language of this science is written. "A fossil," says Sir Charles Lyell, the eminent geologist, "is any body or traces of body, animal or vegetable, buried and preserved by natural causes."

1. Former Ideas about Fossils

Fossil remains of animals and plants, although known from time immemorial, have been variously misunderstood in the

past. To Aristotle they were the artificial results of spontaneous combustion. Empedocles, who found fossil hippopotamus bones in Sicily, thought he had discovered a battle-ground where gods and Titans fought. Henrion, in 1817, regarded fossils as molds and casts left over in the creation of animals and plants, and even as late as 1823, William Buckland of Oxford wrote learnedly "*On Observations on Organic Remains attesting the Action of a Universal Deluge.*" Sir Charles Lyell states that it took one hundred and fifty years of dispute and argument to persuade scholars that fossils were really remains of what were once living organisms, and one hundred and fifty years more to convince them that they were not the results of Noah's flood.

Today a vast number of fossils have been recovered from oblivion in many parts of the world and together they present a most convincing and illuminating mass of evidence concerning the ancient inhabitants of the earth. Even when fragmentary and imperfect, as most of them are, they furnish irrefutable proof of vanished life, just as certainly as the astonishing footprint on the sand of the seashore was as entirely conclusive to Robinson Crusoe that another human being was on his island, as the actual presence of the savage who made it would have been.

2. Conditions of Fossilization

There are various factors involved in the process of fossilization. It is usually essential that fossilizable parts, like bones, teeth, shells, scales, or chitin be present, and that the conditions for natural burial be such as to aid in the preservation of these parts. The great majority of animals and plants do not become fossils, but return at death to their inorganic origins through the route of decay, or by being devoured by animals. Dr. C. D. Walcott has published a book of unexpected facts concerning *Fossil Medusæ*, however, in which are pictured a great variety of these fragile creatures which succeeded in leaving a fossil record of themselves in spite of the fact that their jelly-like bodies had no hard parts, and were over 95% water (Fig. 77).

The manner of burial in fossilization may be sudden and catastrophic, as by landslide, earthquake, devastating flood, overwhelming sand storm, or by a rain of volcanic ashes such as fossilized the entire cities of Herculaneum and Pompeii, or, it may be exceedingly slow, as in the formation of sedimentary rock

under water, the incrustations resulting from immersion in mineral-impregnated hot springs, or by the drip of limy water which forms stalactites and stalagmites in limestone caverns. Quicksands, swamps, and bogs may engulf animals also and thus favor fossil formation by preventing rapid decay through the exclusion

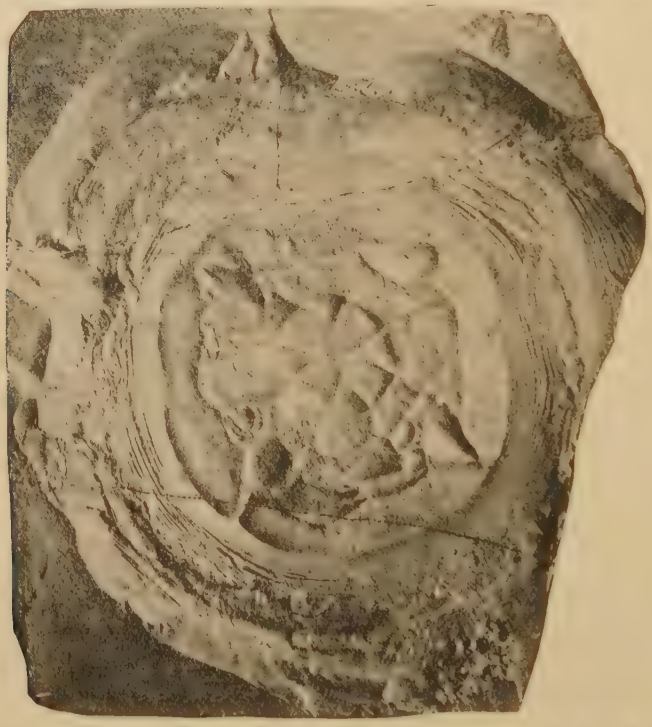


FIG. 77. A fossil medusa, *Rhizostomites*, from the lithographic slate of Solenhofen, Bavaria, showing that even the most delicate organisms may become fossils. [Much reduced in size. The original specimen is in the collection of U. S. Nat. Museum.] (From Walcott.)

of air. As a matter of fact, "bog water" is said to possess antiseptic properties to a remarkable degree. Amber, which is fossilized pitch, furnishes another kind of burial place. Insects, crawling on the trunks of ancient conifers and becoming entangled in the sticky exudations there, succeeded far better than any Egyptian dreaming of immortality, in perpetuating their mortal bodies intact in a world of universal decay. At Rancho La Brea, near Los Angeles, California, there is a famous bed of

asphalt in which at some time long ago a great variety of animals were not only entrapped and killed but also preserved as fossils. In detritus-filled caverns where dying animals have retreated, fossils are frequently found. Sixty miles north of the Arctic Circle at Beresovka in Siberia, a mammoth was discovered in a pit, frozen and so perfectly preserved in ice that some of the flesh was eaten, many thousand years after it was accidentally placed there in cold storage. On oceanic islands with scarcely any rainfall, such as the Chincha Islands off the coast of Peru, where sea birds have long resorted to nest, the dried excreta of the birds, commercially known as "guano," is frequently deposited to a depth of several hundred feet, forming a natural burial place for fossils.

3. Uses of Fossils

Fossils, as Dr. Joseph Leidy many years ago quaintly said of the Protozoa, are chiefly useful as "food for the intellect." Among the various intellectual uses to which fossils are put, not the least is that of "faith testers," so called by good people, alarmed at the silent evidence thus presented of the great antiquity of the earth, which they had been taught to believe was recently created. To the scientist these "medallions of creation" show first of all, something of the *racial history of animals and plants.* In the absence of direct evidence, the past history of most animals and plants must remain largely a matter of conjecture, but there are some modern animals whose ancestral modifications are written very legibly in the fossils that have been found. For example, the horse has a well-established family tree extending backward without serious gaps for at least three million years, to the little five-toed ancestor, *Eohippus,* of the Eocene Formation. The actual fossil evidence for this remarkable pedigree may be seen by any visitor at the American Museum of Natural History in New York City, or at the Peabody Museum of Yale University at New Haven (Fig. 78).

Fossils are useful in the second place as *indicators of past climatic conditions.* The discovery of fossil palms in Wyoming, of breadfruit in California, of ferns in Greenland, of reindeer in France, and of musk oxen in Kentucky, for instance, record the indisputable fact that profound changes in climatic conditions have occurred in all these places in the past.

Fossils serve also as *measures of geologic time.* Just as the date

upon a corner stone indicates the period when a building was erected, so the presence of certain types of fossils in a particular stratum of sedimentary rock, indicates the approximate time when those rocks were laid down. Or, to state the value of time

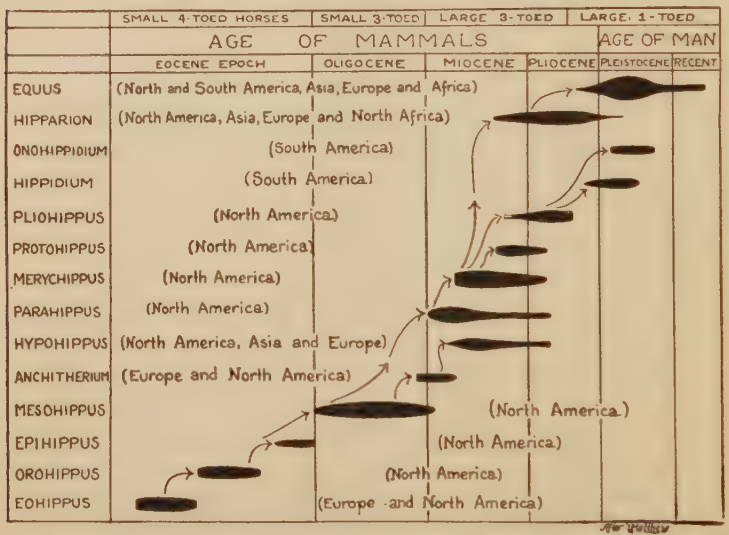


FIG. 78.—The evolution of the modern horse, *Equus*. (After Matthew.)

measure by a further comparison, just as the character *f* instead of *s* on a page of an old book measures the limits of its publication by the date 1800, about which time the character *s* came into general use, so the presence of a time-fixing fossil on a geologic page measures the limits of its formation.

4. Kinds of Fossils

The following classification of the different kinds of fossils is modified from that given by Professor R. M. Field.[1]

I. Those furnishing direct evidence:—

1. Actual remains, such as insects in amber, mammoths in ice, or shark's teeth.
2. Minute replacements, replacement molecule by molecule of the original organic matter by mineral salts, resulting in *petrifaction*, which may or may not show structure.
3. Coarse replacements, molds and casts of exterior or interior structures.
4. Prints, of leaves, jellyfish, etc.

[1] *Science*, June 25, 1920.

II. Those furnishing indirect evidence:

1. Coprolites, that is, solidified excreta, or casts of same.
2. Artifacts, such as ant hills, or prehistoric flints.
3. Tracks, trails, and burrows.

III. SOURCES OF IMPERFECTION IN THE GEOLOGIC RECORD

The absence of suitable conditions for fossilization which surround the passing of the vast majority of animals and plants, and the inaccessibility of most of the fossils that actually succeed in being formed, make the task of the palæontologist a particularly difficult one. The pages of the great stone book cannot be shuffled over in order to read the story contained therein, because they are stuck firmly together. The fossil writing is quite inaccessible except as lucky chance reveals enticing fragments of it, as when slow erosion bevels down the margin of the page, exposing thus some few organic syllables, or when, by the puny engineering feats of man the surface of the earth is somewhere scratched open, accidentally uncovering some of its buried treasures.

In many instances the natural sequence in rock formation has been confused so that the student finds the pages of his book misplaced, by distortion or folding as in mountain formation. The more recent strata sometimes even come to lie beneath the older ones. The irregular and fragmentary character of the fossiliferous strata thus greatly increases the difficulties that confront the student who would correctly read the story of the past. Moreover, sedimentary rocks of the earth's crust containing fossils are not arranged in continuous strata that envelop the entire globe with regularity like the layers of an onion, but they form in patches of unequal thickness and extent according to the distribution of the water areas at the time of their deposition.

Furthermore, there is no doubt that the earlier records of life in the form of fossils have in many cases been entirely obliterated by the action of heat and pressure during the metamorphosis of rocks into such forms as gneiss and granite, while fossils that are buried in sedimentary rocks of the ocean floor are "forever hidden from hammer and mind."

According to the Bureau of Mines, Department of the Interior,[1] the deepest hole that man has ever made in the undisturbed

[1] *Science*, N. S., LX. No. 1541.

fossil-bearing epidermis of the earth, is in West Virginia, where it was bored to a depth of 7,579 feet in search of natural gas. The deepest mine in the world, a vertical depth of 6,726 feet, is the St. John del Rey mine in Brazil, while the "Village Deep" workings of the gold mines of Transvaal, South Africa, take second rank, extending to a depth of 6,263 feet. In the United States the deepest mine workings are those of the Calumet and Hecla Consolidated on the Keeweenaw Peninsula, Michigan, 5,990 feet below the surface. This, a distance of only 4,000 feet below sea level, represents the nearest approach man has ever made to the center of the earth. These extraordinary depths of a little over a mile, however, when compared with the total diameter of the earth (nearly 8,000 miles) or even with the known thickness of sedimentary fossiliferous rocks are so insignificant that it is doubtful if it could in any way be graphically represented to scale on a four-foot globe. David Starr Jordan has truly said that the case of the palæontologist is much like that of a traveler who, landing for five minutes on some remote corner of Australia, forthwith attempts a description of the entire continent. The wonder is not that so little is known of the fossil record of animals and plants, but that, in the face of so many difficulties, so complete and connected a story of ancient life has been unearthed.

IV. A GEOLOGIC TIME SCALE

The fragment of eternity that comes within the vision of the geologist has been divided into unequal *eras* of time, beginning after the earth had cooled down enough to be clothed with an atmosphere and to have its surface diversified into areas of land and water. The succeeding eras are measured by the time taken to form stratified rocks through the disintegration and erosion of the original fire-fused rocks, and the subsequent rearrangement of their component particles as sediment under water. Such sedimentary rocks afford sanctuary to organic remains and form the happy hunting ground of palæontologists. These eras, from ancient to modern are:—ARCHÆOZOIC, PROTEROZOIC, PALÆOZOIC, MESOZOIC, and CENOZOIC.

The *Archæozoic Era* is characterized principally by igneous and metamorphosed rocks without proved fossils, although traces of graphite indicate that plant life must have been already in existence. The fiery furnace that fashioned the Archæozoic rocks,

however, was no suitable place for the preservation of whatever organic remains existed in those formative days.

The *Proterozoic Era* saw the slow rise of the lower plants and most of the main general types of invertebrate animals. Together with the Archæozoic Era, according to Professor Schuchert, it constitutes over one half of the total column of known sedimentary rocks, which reaches a maximum thickness of 114 miles in North America, although he qualifies this statement by saying, "In no one place, however, can be seen more than a small part of this record, for usually the local thickness is under one mile, though there are limited regions where as much as twenty miles of it is present."

The *Palæozoic Era* has been called the "Age of Fishes" because these animals became dominant during this time. The actual interval which elapsed in the Palæozoic Era has been estimated by Dr. Walcott as 17,000,000 years, surely sufficient for many dynasties of plants and animals to have had their day.

A Geologic Time Scale (Schuchert)

Era	% of Geol. Time	Period	Characteristic Features
Cenozoic	4.4	Quarternary	Last great ice age.
		Tertiary	Transformation of apes into man.
			Rise of higher mammals.
Mesozoic	13.4	Cretaceous	Rise of archaic or primitive mammals.
		Commanchian	Rise of flowering plants and higher insects.
		Jurassic	Rise of birds and flying reptiles.
		Triassic	Rise of dinosaurs.
Palæozoic	27.8	Permian	Rise of reptiles. Another great ice age.
		Pennsylvanian	Rise of insects. Marked coal accumulation.
		Mississippian	Rise of marine fishes.
		Devonian	First known amphibians.
		Silurian	First known land floras.
		Ordovician	First known fresh-water fishes.
		Cambrian	Abundance of marine animals, and dominance of trilobites.
Proterozoic	15.0		An early and late ice age.
Archæozoic	39.4		Origin of protoplasm and of simplest life.
	100.%		

Following the Palæozoic, the *Mesozoic Era* witnessed the "Golden Age of the Reptiles," some 7,000,000 years according to Walcott; and finally the *Cenozoic Era*, or "Age of Mammals," probably representing a little more than 3,000,000 years.

The most recent episode in all this great moving spectacle of earth transformation is *human history* extending over a few thousand years at the outside, which, in comparison with the stretches of time under consideration, is but the thinnest surface film on the face of an abyssal ocean.

The table on page 95 gives a geologic time scale, with the periods in which the various eras are subdivided in America, and a hint of the characteristic organisms that flourished in each of these hypothetical divisions of time.

V. PICTET'S PALÆONTOLOGICAL LAWS

A summary of some of the more important conclusions which result from a study of fossils is embodied in six "laws" adapted from *Traité élémentaire de palæontologie* by Jules François Pictet (1809–1872), as follows:

1. All stratified rocks may contain fossils, therefore, *life has been present on the earth for a very long time.*

2. The oldest strata contain extinct species and largely extinct genera, while more recent strata contain forms like the living, therefore, *the deeper the stratum the more divergent are the forms found therein from those now living.*

3. Different fossil faunas and floras follow each other in the same sequence everywhere, and layers nearest together stratigraphically contain forms most alike, therefore, *fossils show the evolution of forms one from another on the earth.*

4. Constant change is the inevitable law of life. Species characteristic of one level or time are partly or completely replaced later by other species, therefore, *species are not permanent or unchanging but are constantly giving way to modified forms that are presumably better qualified to occupy their place in nature.*

5. Species, as well as individuals, pass regularly through a cycle, including infancy, youth, maturity, and senility, therefore, *many groups of organisms have died out entirely, having completed their cycle,* for example, graptolites, trilobites, and ammonites.

6. The approximate age of any stratum may be determined by the degree of similarity of its fossils to living forms. Similar fossils in different regions are indications of geologic strata of contemporaneous formation, therefore, *fossils serve to determine the age of the rocks in which they are found.*

CHAPTER V

THE ANCIENT HISTORY OF MAN (ANTHROPOLOGY)

I. THE IDEA OF ANTIQUITY

One of the famous riddles that perennially charms and challenges us, is the origin of mankind upon this earth, for the farther back we go the more vague is our knowledge about man. As a matter of fact it would be much easier to consider the *iniquity* of man than his *antiquity*, for then we would find abundant material at hand for our discourse. The subject of the antiquity of man must always remain more or less shrouded in mystery. The reality of human antiquity, however, even in the absence of specific details, is beyond question, as may be pointed out by an individual illustration.

The writer was born sometime in the nineteenth century. In the eyes of the children of the twentieth century he must seem quite old. He can even remember when there was not a single automobile in existence. He has lived through the entire Golden Age of the bicycle and participated in its rise and fall. He recalls when there was no radio, no telephone, no phonograph, no electric lights, no typewriters, no motion pictures, and when the *Darius Green and his Flying Machine*, of John T. Trowbridge, represented the final word in aviation. He remembers his grandparents as very old people, associated with ox teams and candle-light, for they were babes in arms when the War of 1812 was being fought. Their grandparents in turn lived before the Revolutionary War and even traditions about them are now vague and hazy. Beyond them there must have been others, but they lived so long ago that the present day has entirely lost sight of them.

It is quite possible, however, after the personal ancestral thread thus vanishes in the distant past, to resort to the pages of history and to push back in imagination to such hoary landmarks of time as the discovery of America, the Norman Invasion, the dramatic beginning of the Christian Era, and even beyond these milestones to remote semi-mythical days when the Ten Thousand beat

their famous retreat, or the Children of Israel passed dry-shod through the Red Sea, or when Tutankhamen was living flesh instead of a fashionable mummy.

But the palæontologist laughs in his sleeve at anyone who pauses to consider such contemporary events, while the astronomer in turn, dreaming of the majestic march of worlds other than ours, pities the palæontologist who is content to think about such slight fragments of time as geologic ages. How far back into the shadowy past can the flickering torch of humanity be traced? What are the facts about the antiquity of man? Was there ever a time so remote that man was not man but something else? The sciences of *Anthropology* and *Prehistoric Archæology* are concerned with questions such as these.

II. TRADITION AND EVIDENCE

Various traditions of human origins are a part of the folklore of every racial stock. The most familiar of these traditions is probably that of Adam and Eve, in which man is created "of the dust of the ground." Another classical legend of the inorganic origin of man is that of Deucalion and Pyrrha who, at the suggestion of Jupiter, peopled the earth by simply throwing stones over their shoulders, the stones becoming men or women according to which one of the celestial pair did the throwing. If these wonder workers had chanced upon a typical glacial hillside of New England, instead of the summit of Mount Parnassus, no doubt the overpopulation problem would be much more acute than it is today. The Greek and Roman classics are full of tales of dryads born of trees, and of Galateas coming to life from cold marble or lifeless ivory. Such stories and traditions, however, are in no sense *evidences* of the actual origin and antiquity of mankind upon the earth. These evidences must be sought for in less romantic historical records and indirect testimony of various kinds from other sources.

In America historical records of man practically date from the conquest by the whites only a few centuries ago, although there are strange architectural remains in Mexico, Central America, and Peru, that mark the presence of earlier, but highly advanced civilizations, now vanished. In Europe man was in a condition of unrecorded savagery long after he had attained a high degree of development elsewhere. Recorded human history goes back

with undoubted assurance only about 5,000 years and then, in Egypt and Mesopotamia, continues with halting steps for perhaps 2,000 years more, after which the historical record fades and it becomes necessary, in tracing the antiquity of man, to resort to the unwritten evidences of *prehistory*.

The prehistoric evidences of human antiquity may be grouped into five categories, as follows:

(1) Indirect evidence from the length of time during which the earth has been habitable by man.
(2) Indirect evidence from the amount of time which must have elapsed in order to allow mankind to reach its present degree of development.
(3) Direct evidence from various discoveries of actual prehistoric human bones.
(4) Indirect evidence from telltale fragments of extinct animals found associated with human remains.
(5) Direct evidence from the enduring handiwork of man.

Some brief explanation and elaboration of these different lines of evidence is necessary to make their content clear.

III. THE HABITABLE EARTH

Astronomers, physicists, and geologists all testify to an unthinkably remote period of time since the stage has been set for human life upon this earth. It does not necessarily follow that man appeared as soon as the earth was ready for human occupancy, but this testimony does remove any objections to the antiquity of man on the score of possible geological unpreparedness with regard to his abiding place.

Professor Rutherford, from calculations of the rate of radioactive transformations, estimates the earth as at least 240,000,000 years old, while Lord Kelvin, reckoning the rate of heat loss from the earth, makes its age as between 20,000,000 and 400,000,000 years. Professor Sollas finds 80,000,000 years none too much to have accomplished the known weathering of the rocks and their deposition as sedimentary strata, while the same length of time has been independently computed as necessary to allow for the leaching out of the earth's crust enough to make the oceans as salty as they are today. The discrepancies which appear in these dizzying time estimates of various experts, who have thus contributed to the problem of the age of the habitable earth, may be

disregarded as irrelevant, since they all agree in furnishing a cradle for humanity that is an unquestionable antique.

IV. THE TIME REQUIRED

Anatomically the human body is an "old curiosity shop" of parts that are present in varying degrees of perfection. There is every indication that the process of adaptation is still going on, and that the human body as we see it today is the result of repeated changes that have taken place in the past. There is no part or structure of a human being which is not foreshadowed in the lower animals. The tracing out of resemblances and sequences in structure and organization between different animals and man, is the particular province of *Comparative Anatomy*, and the facts that constitute the working basis of this science furnish undeniable evidence bearing upon the antiquity of man. Just as the modern ocean liner, with its luxurious appointments and efficient, intricate machinery, implies years of invention and experimentation with preliminary boats of a lesser order of elaboration, so the four-chambered heart, larynx, or brain of man, to anyone who knows intimately about the detail and complexity of these organs, tells a long story of preparatory variation and adaptation that must have required an enormous length of time for its accomplishment.

The science of *Chorology*, or the geographical distribution of animals and plants over the face of the earth, furnishes abundant evidence of the antiquity of man of an undeniable kind. The spread of human beings to the uttermost corners of the earth, which we recognize as an accomplished fact, could never have occurred by any series of successive migrations without involving considerable lapses of time.

Two other sciences, *Ethnology* and *Philology*, also bespeak the necessity of an extended period of past time for the existence of man, in order to account for present results.

Ethnology deals with various *races* of man, and with his customs and institutions, while philology is concerned with human language and its evolution. In both these fields humankind has attained a high degree of specialization which, when one attempts to disentangle the various steps that must have preceded it, takes one back so far that there can be no doubt about the great antiquity of man. The evidence of ancient monuments and of

history all goes to prove that the great race divisions of mankind are of no recent growth, but were already settled long before the beginning of the historic period.

As for language, each of the branches of the so-called Aryan group of primitive languages, Persian, Indian, Semitic, Romance, Hellenic, Slavonic, Teutonic, and Keltic, has its roots buried in antiquity. The Hebrew and Arabic, for example, are both ancient and neither the original of the other, but both are derived from some ancestral source.

V. HUMAN FOSSILS

The actual bones of prehistoric man furnish, of course, the best direct evidence of human antiquity, but, unfortunately, they are very scarce. This is in part due to the arboreal life which early man lived, rendering dead bodies likely to be devoured on the spot or subject to immediate decay. Moreover, a large part of the earth, including many localities where human remains might have been overwhelmed and fossilized, has not as yet been thoroughly explored by competent scientists. The eminent French palæontologist, Cuvier, as late as 1852, pronounced the famous dictum, backed by his extensive knowledge, "*L'homme fossile n'existe pas.*" All the supposed discoveries of prehistoric remains up to that time had been shown to be of comparatively recent origin or not human at all. One oft cited case is that of Scheuchzer, who found and described in 1732 a "fossil man" to which he gave the name of *Homo diluvii testis*, or "man, witness of the flood," and upon which he piously commented as follows: "Rare relic of the accursed race of the primitive world. Melancholy skeleton of an old sinner preserved to convert the hearts of modern reprobates!" This turned out, however, to be not a human skeleton at all but the bones of a giant salamander.

In 1856, about the same time when Darwin's *Origin of Species* (1859) appeared, throwing both the scientific and the theological worlds into intellectual convulsions, the famous *Neanderthal Man* came to light. This is an incomplete human skeleton unearthed by workmen in a detritus-filled cavern high up on the precipitous side of a ravine about sixty feet above a stream and a hundred feet below the top of a cliff near Düsseldorf, Germany. With the skeleton was found, embedded in hard loam, the bones of animals long extinct, the cave bear, mammoth, cave hyena, woolly rhinoc-

eros, and others, and the superimposed detritus covered over by strata of undisturbed sedimentary rock, put the seal of unquestionable antiquity upon the time when the Neanderthal Man lived. The bones themselves, which have undergone more expert scrutiny than perhaps any other set of bones, indicate a burly, squat, bow-legged individual with a thick skull, projecting brows, low retreating forehead, and receding chin, characteristics distinctly different from those of modern man. That the Neanderthal Man was not a unique prehistoric hermit has been unquestionably demonstrated by the discovery, during the past half century in various localities in Europe of at least a score of individuals represented by bony fragments of one kind and another, all agreeing essentially with the original find. The existence of a race of human beings, *Homo neanderthalensis*, unlike modern man, or *Homo sapiens*, is now no more in doubt than the existence of ancient Egyptians.

Human bones, however old, showing signs of burial by man probably nearly all fall within the period of historic time and do not enter into the present inquiry, but there are at least three other kinds of human beings known to science between the Neanderthal race and modern man, which have left definite skeletal traces of themselves behind. They are the *Grimaldi*, *Cro-Magnon*, and *Aurignacian* types.

The Grimaldi are represented by two skeletons, a woman and a young boy, found in 1906 in a cave at Mentone, southern France, together with a snail-shell necklace and bracelets. They are negroid in character with narrow skulls, projecting cheek bones, and prognathous jaws, but, according to the testimony of experts, anatomically unlike any other known human beings before or since.

The Cro-Magnon race, or the reindeer hunters, lived about 25,000 or 30,000 years ago near the close of the last Ice Age. They were tall, finely built specimens of humanity, with large skulls. They not only left some of their bones behind but also mural decorations, for they were primitive artists of considerable skill, as the "painted grottoes," to be mentioned directly, attest.

The Aurignacians were likewise mighty hunters, principally of wild horses, as well as grotto decorators of no mean ability, like the Cro-Magnons. They were scattered over what is now Europe somewhat before the time of the Cro-Magnons. In the Rhone

Valley, for instance, at Solutré near Lyons, is an area of five or six acres where the bones of extinct horses, reindeer, and mammoths have been found, in places to the thickness of several feet, along with the remains of Aurignacian hunters and their flint weapons.

Anthropologists seem to agree that these several types of prehistoric men are not direct descendants of the Neanderthalers, but probably migrated into Europe from some other regions of the globe where their forebears had been working out their slow salvation from lowly origins. It is, moreover, not at all certain that *Homo neanderthalensis*, or either of the subsequent types just mentioned are the direct ancestors of *Homo sapiens* of today who goes back through historic times as far as the shadow of the last great Ice Age.

It is estimated by Osborn that the Neanderthal race, "contented to live 50,000 years in caves," flourished from 30,000 to 100,000 years ago. There are, however, at least two famous witnesses of human antiquity that antedate the Neanderthalers. They are the "Dawn Man," *Eoanthropus dawsoni*, probably of the Third Interglacial Stage, about 150,000 years ago, and *Homo heidelbergensis* of the Second Interglacial Stage, perhaps 250,000 years ago, well back towards the beginnings of the Pleistocene Period of geological chronology.

The *Eoanthropus* skull fragments, pronounced by G. F. Scott Elliot as "perhaps the most fortunate discovery of all yet made," were found by Dawson in 1911 at Piltdown Common near Sussex, England. With them were flint tools of extremely primitive character and certain animal remains, like the teeth of the hippopotamus, horse, and ancestral beaver, together with fragments of two kinds of extinct elephants that flourished in the early Pleistocene, or even Pliocene times. The anatomical evidence, particularly that furnished by the lower jaw, shows the Piltdowner to have been more apelike than the Neanderthalers, and certainly distinct from *Homo sapiens*. The skull is probably that of a female, who, according to Professor G. Elliott Smith, was possessed of the power of speech, "just like woman of today." The belief has been expressed that *Eoanthropus* represents the ancestral line of the Aurignacian race, but in spite of a crowded ten-foot shelf of learned papers upon the subject, much uncertainty about the ancient woman of Piltdown still exists.

There is less controversy in fixing the degree of antiquity of *Homo heidelbergensis*. This race is represented by only a lower jaw, found by Schoetensack in 1907 buried in a gravel pit near the mouth of the Neckar River Valley, not far from Heidelberg, Germany, under conditions that proclaim it to be unmistakably the oldest known authentic human fossil (Fig. 79). Over seventy-nine feet of undisturbed sand and sedimentary rock had been slowly deposited upon this interesting ancestor, and subsequently, by the slow eroding action of the Neckar River, worn away in the formation of the Neckar Valley, before this famous human fragment was eventually exposed to modern view (Fig. 80). The jaw

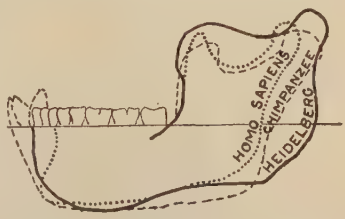


FIG. 79.—Outline of the Heidelberg jaw, contrasted with that of the chimpanzee and man. (After Boule.)

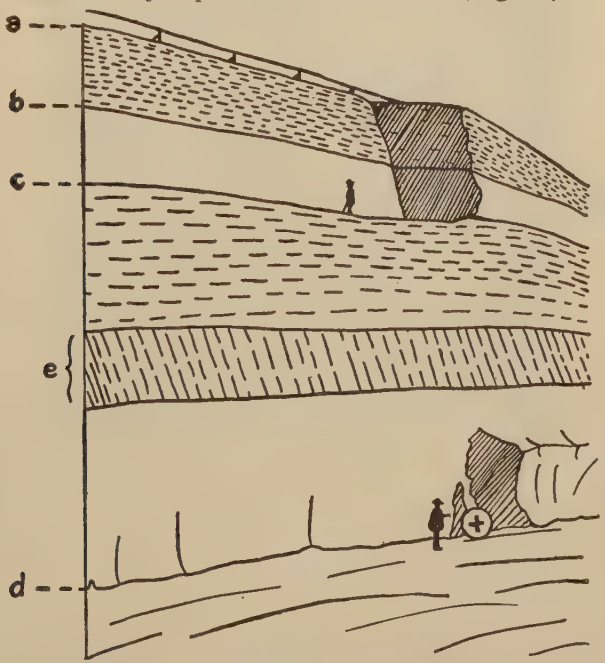


FIG. 80.—Diagram of the sand pit where the *Heidelberg jaw* was discovered. *a–b*, layer of "Newer Loess"; *b–d*, "Older Loess"; *c–d*, Mauer sands; *e*, clay. The cross indicates the spot under seventy-nine feet of undisturbed strata where the fossil jaw was found. (After Schoetensack, in Osborn's *Men of the Old Stone Age*. Charles Scribner's Sons.)

is heavy, massive, and chinless. An apelike genial pit and characteristic encroachment of bone upon the floor of the mouth, together with the broad ramus that is peculiar to the lower primates, are present, but the teeth are comparatively small and have the shortened roots and dilated crowns which distinguish human

FIG. 81.—Gabriel Max's famous imaginary conception of a *Pithecanthropus* family group. (From heliograph copy by Meisenbach, Riffarth & Co.)

teeth from those of lower animals. With the discovery of the Heidelberg jaw, the skeletal evidence of the antiquity of man is pushed back something like a quarter of a million of years to the early part of the Pleistocene Period.

VI. BONES OF CONTENTION

The fossils considered in the preceding paragraph are conceded to be evidently human, although the older the fossil, the more it resembles the apes. But what lies back of primitive man? Who

were Adam's ancestors? All the evidence from anthropology leads one to postulate fore-runners of mankind that were not human.

The German zoölogist, Haeckel, was so confident that such a kind of beings once lived that in 1866 he assigned the name, *Pithecanthropus* (ape-man), to the unknown, and prophesied its future discovery. Haeckel's conception of an ape-man so fired the imagination of the artist, Gabriel Max, that the latter produced a famous painting of a Pithecanthropus family group which is reproduced in Fig. 81. Of course this picture is wholly imaginary and unscientific in being entirely without any basis of direct evidence. In 1891, however, Professor Dubois, then an officer in the Dutch army stationed in Java, found fossil remains on one of the banks of the Bengawin River near Trinil, that fulfilled Haeckel's expectation. These remains were a skull-cap, or *calvarium*, and a molar tooth to which later were added, from the same locality, a left thigh bone and two other teeth, together with a fragment of the lower jaw that has not yet been technically described in detail. Companion bones that filled four hundred boxes were unearthed with these celebrated relics and brought back to Holland, including bones of the extinct proboscidian, *Stenodon*, the ungulate *Leptobos*, *Hyæna*, *Hippopotamus*, and Giant Pangolin, no longer inhabitants of that part of the world, as well as tapirs, now found only in South America, on the

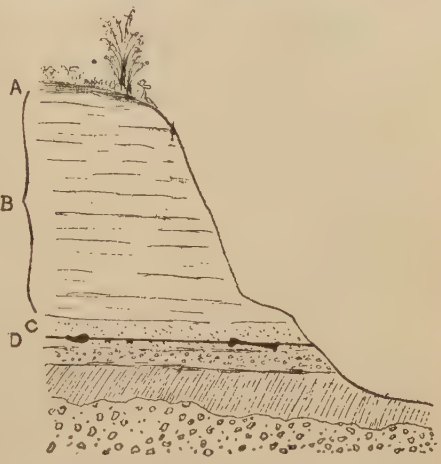
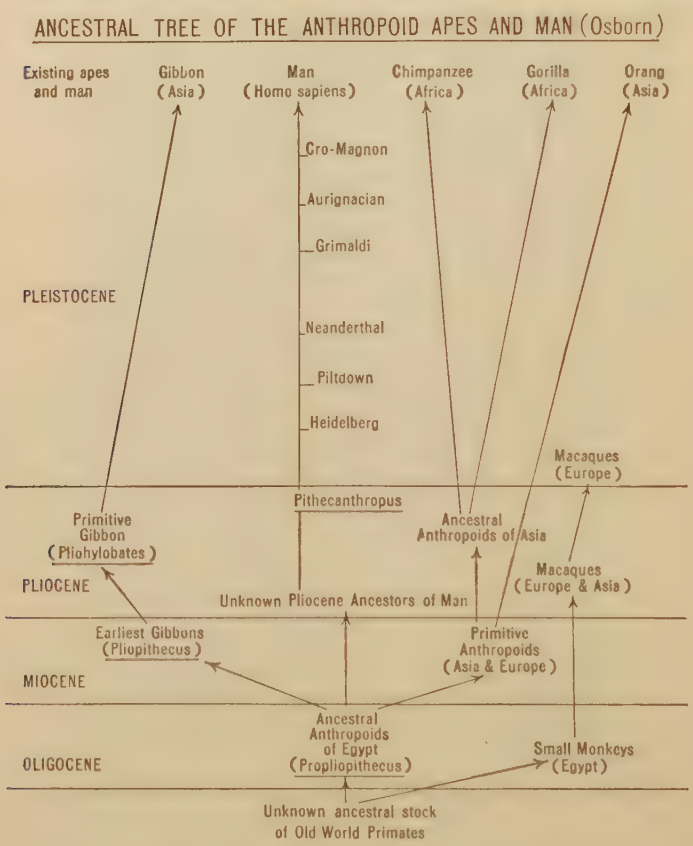


FIG. 82.—Diagrammatic cross section through the fossiliferous strata in Java where the *Pithecanthropus* bones were found. *A*, surface soil; *B*, undisturbed sandstone; *C*, volcanic layer; *D*, level of the *Pithecanthropus* bones and of various extinct Tertiary animals. (After Dubois.)

FIG. 83.—A comparison of the skull capacity of various primates. (After Boule.)

other side of the globe. Altogether twenty-four species of Tertiary (Pliocene) animals, under forty-five feet of undisturbed stratified deposits have been identified among these remains, fixing the time when this creature lived as approximately 500,000 years ago (Fig. 82). The fragments of *Pithecanthropus* were recovered some



twenty yards apart, thus disproving any likelihood of intrusive burial. The thick skull, which shows heavy projecting supra-orbital ridges, has a capacity of not far from 900 cubic centimeters (Fig. 83). That of the largest ape is only about 600 cu. cm., while that of modern man fluctuates between 1250 and 2,000, with an average of perhaps 1,450.

It is probably incorrect to regard *Pithecanthropus* as living strictly up to its name, "ape-man," and forming a "connecting

link" between the apes and man, for both apes and man no doubt go back in converging ancestral pathways to some unknown humbler origin common to each. Apes and monkeys are, in all probability, not the fore-runners of mankind, but side lines off the highway of human derivation. Klaatsch, who speaks from a profound knowledge of comparative anatomy, describes apes as "unsuccessful attempts to compass the road to mankind from prehuman stock." It is quite as likely, therefore, that apes are descended from man, as that man is descended from the apes. Young apes, in fact, resemble human beings very much more than do the adults, for as they grow older the more apelike and the less human they become, and fossil apes of the Miocene and Pliocene are more like man than their living descendants today. Probably this evolution in the lifetime of the individual ape pictures roughly the long transformation that has been wrought in the slow procession of species. Although it may be unwarranted to link apes and man in lineal relationship, the conviction must remain that in *Pithecanthropus* we have the only bridge at present known which joins man directly with his non-human ancestors.

The table on page 108 is an attempt to indicate the probable relationships of the better known primates and their distribution in time.

VII. TELLTALE FOSSILS OF EXTINCT FORM

Prehistoric man, like his historic followers, is known by the company that he keeps. As already indicated his bones have been found together with the bones of fearsome beasts long extinct or strangely different from the animals that now inhabit the same parts. The hairy mammoth, *Elephas primigenius*, and the mastodon, *Elephas antiquus*, as well as proboscidians older yet, *Elephas meridionalis* and *Elephas mercki*, were conspicuously present. At Predmost in Moravia there is a hill of "lœss formation," made up of peculiar accumulations of clay, containing so many mammoth bones that it has been profitably mined as a source for fertilizer. From this locality alone over 2,000 of the gigantic compound cheek teeth of mammoths have been taken.

Other ancient contemporaries of man were the huge *Rhinoceros etruscus* and its woolly relative, *Rhinoceros tichorinus*, the cave hyena, *Hyæna spelæa*, the cave lion, *Felis spelæus*, and the cave bear, *Ursus spelæus*, perhaps the fore-runner of the grizzly. The

abundant bones of wild horses, wild boars, and reindeer all over that part of Europe where most of the fossil remains of man have been found, are eloquent witnesses of an ancient régime when man lived in a different world than that of today. In southern France alone there were eighteen species of animals which were formerly abundant but have now migrated to climes more congenial to them. Of these, thirteen, like the reindeer, have gone north, and five, like the chamois and mountain goat, have retreated to cool mountains.

VIII. ARCHÆOLOGICAL CHRONOMETERS

In some instances the handiwork of man has endured for a longer time than his actual bones. This is particularly true of the "indestructible flint" tools and weapons which he fashioned. The more important evidences that come from the field of *Prehistoric Archæology* may be summarized under the following headings: kitchen middens; pile dwellings; painted grottoes; monuments of various kinds; and fashioned flints.

1. Kitchen Middens

Kitchen middens are ancient garbage dumps where prehistoric men congregated and feasted. They were first described from Denmark by Thomsen, in 1836, and have since been found in other localities as widely separated as Japan, Spain, Brazil, California, Oregon, Maine, British Columbia, the Aleutian Islands, Terra del Fuego, the north coast of Africa, and the shores of the Baltic Sea. They consist principally of enormous masses of shells that could not have been collected together by any natural agency, and they usually occur near the seashore, or where the seashore once was, because there primitive man had easy access to his shellfish food supply.

Mingled with shellfish remains are significant archæological treasures of various kinds,—teeth, scales, bones of animals eaten, fragments of crude pottery, anvil stones, hammers, implements, and ornaments of different sorts made out of stone, horn, obsidian, and flint, while pieces of burnt wood and flat stones blackened with fire, indicate, even to an amateur archæological Sherlock Holmes, the use of fire by the people who left these extensive piles of refuse.

Some of the shell heaps, as those on the coast of Maine, for

example, do not bear the earmarks of great antiquity, but probably date back simply to pre-colonial Indian days. Other kitchen middens, however, as those of the Baltic region, contain internal evidence of great age, for they consist largely of shells of salt-water molluscs which cannot grow in brackish or fresh waters that characterize the Baltic Sea today, but must have flourished long ago when there was an open communication between the Baltic and the salt ocean.

2. Pile Dwellings

The Greek historian Herodotus gives a detailed account of Thracian aborigines who dwelt in rude huts built upon piles out in the waters of Lake Prasias in the land that is modern Rumelia. The most interesting exponents, however, of this style of semi-aquatic architecture are the still older lake dwellers who lived and died perhaps some 6,000 years B.C., just beyond the outer halo of history. They represent a primitive type of vanished civilization that came to flower particularly in the general region centering in Switzerland where they erected their pile dwellings along the margins of the numerous Alpine lakes.

Since a year of great drouth and low water in 1854, when the submerged ruins of some of these curious pile dwellings came to light in Lake Zurich, a large number of the sunken remains of pile-built settlements have been discovered, and from the mud around a great number and variety of relics have been recovered, that make possible a fairly complete picture of the kind of life which these ancient lake dwellers lived (Fig. 84). The sites of over 200 of these prehistoric villages have now been located in the Swiss lakes alone.

The pile dwellers represent a decided advance over the precarious, nomadic life of the cave dwellers who preceded them. Building thus together upon piles over the water enabled them to establish a haven of comparative safety from the assaults of hostile marauders and ferocious beasts, and furnished the security and leisure necessary in making initial steps in invention, and the arts of peace and organized warfare.

Moreover, living over the water doubtless insured some degree of primitive sanitation unknown, or at least unlikely, among those who pitched their camps in caves and forests upon land, for consequences following in the wake of sanitary carelessness must have

been quite as inevitable then as in these latter days when the bacteria of disease have been discovered and named by man.

In the *Antiquarisches Museum* in Zurich is a particularly noteworthy collection of the prehistoric handiwork of the vanished pile dwellers.

3. Painted Grottoes

About the time of the reindeer occupation of what is now France and Northern Spain, there flourished a remarkable period of pre-

FIG. 84.—Reconstructed Lake Dwellings. (From Tyler's *New Stone Age in Northern Europe.* Chas. Scribner's Sons.)

historic art, represented chiefly by crude drawings and paintings upon the protected walls and ceilings of caverns.

Although these treasures were first discovered and made known within the memory of persons now living, there already have been catalogued from these troglodytic art galleries nearly 3,000 different pictures. In the Dordogne region of France, for example, one cavern alone, the "Combarelles," is a veritable prehistoric Louvre, containing 109 wall pictures, which cover an area of over 2,000 square feet. The pictures are mostly outlines of animals,—bison, reindeer, mammoths, wild horses and others, that were contemporary in Europe with the cave-dwelling, flint-using folk who drew them, and usually they are well enough done to be un-

mistakable. The most ancient of them, apparently the work of the Aurignacian hunters, are bare outlines, roughly engraved on the cavern walls by means of flint tools, and probably in the light of flickering torches. However, the best of these old animal pictures, as well as the majority of them, were evidently made later by the Cro-Magnon people, and are for the most part flat surfaces chipped into the solid rock and colored with various substances such as chalk, charcoal, red and yellow ochre, or other mineral pigments. The famous polychrome frescoes of the Altimira caverns in Spain, which would be a credit to artists of a much later time, mark the highest point of excellence. The fact that the most recent cave drawings were considerably inferior in their execution to the earlier ones, indicates that the ability for artistic expression was an inborn characteristic of the Aurignacians and Cro-Magnons, which faded with the passing of these prehistoric hunters.

The approximate age of the painted grottoes is determined by the kind of bones and flint implements found in the rubbish that filled the caverns, in this way protecting the pictures from exposure and destruction, and by certain other timemarks, such as paintings of different dates superimposed one above the other. All in all, these early attempts at artistic expression are direct evidences of the great antiquity of man, for only man, of all creatures, could have left such signs of the times.

4. Monuments

The ancient Egyptians who built pyramids, sphinxes, and obelisks in the attempt to outwit the devastating tooth of time, were not the first of mankind who desired to leave some enduring memorial of themselves for succeeding generations to see. Prehistory, as well as written history, bears witness to the same human desire for impressing posterity. This desire has found expression either in the form of large stones, *megaliths*, arranged and set up in various unnatural ways, or in the form of mounds or earthworks of unmistakable human workmanship.

Large columnar stones set up on end are called *menhirs*. Of these over 700 have been located in Brittany alone. Primitive man must have exercised a good deal of engineering skill, probably by digging pits, building temporary inclined planes, and using pulleys of some sort, in order to jockey these huge stones into

position. Their size and shape precludes their present placement by any natural agency.

Frequently menhirs were set up in parallel rows, termed *alignments*, or in circular arrangement, designated as *cromlechs*. A flat stone resting upon two uprights is called a *trilith* but when several uprights support a top stone, like a rude table or altar, the structure is called a *dolmen*. Nearly 5,000 dolmens have been found in France, while in England at Stonehenge and at Avebury there are two very famous and much described collections of

FIG. 85.—Two prehistoric Easter Island statues. (After Mrs. Scoresby Routledge, in the *National Geographic Magazine* for December 1921.)

megaliths, arranged as alignments, cromlechs, dolmens, and single menhirs. The collection of megaliths at Avebury is more extensive than that at Stonehenge, but it is not as well preserved because the stones were largely removed in building the modern village of Avebury. A cromlech 1,200 feet in diameter, made up of 100

separate stones each seventeen to twenty feet high, forms a part of the Avebury collection.

Some of the most curious and mysterious evidences of ancient human activities are the stone images of Easter Island (Fig. 85). On this isolated island in the South Pacific, 2,000 miles west of South America, there are over 600 stone statues, hewn out of volcanic tufa and weighing from three to thirty tons each. They are all patterned alike, regardless of size, and represent a half-length human figure with hands placed across the front of the body. Not one of the statues was found upright. They had all been overturned since they were originally set up, and the present inhabitants of Easter Island do not even have traditions as to their origin. Altogether they form one of the most puzzling of archæological enigmas.

In addition to megalithic witnesses of human activity in the distant past are *mounds*, *tumuli*, and *earthworks* of various sorts, that tell the same story of the antiquity of man. Some of these structures were no doubt connected with ancient burial customs or religious ceremonials, while others were probably once places of refuge, or fortresses, the ruins of which remain to remind us of the gray days during which our distant ancestors kept alive on the earth the precious spark of humanity.

5. Tools and Weapons

Man, of all animals, is the only one adapted for grasping tools or weapons. The tools and weapons of other animals, such as horns, teeth, tails, and claws, are a part of the permanent equipment of their possessors and may be improved or substituted for other tools only in the slow workshop of adaptive evolution. Exchangeable instruments in the grasp of the hand of man have enormously increased the sphere of his possible activities.

Some of the earliest tools and instruments fashioned by man furnish direct evidence of human antiquity that antedates his oldest fossil remains. This type of evidence is far more accurate and reliable than any historical chronicle whatsoever that has been colored by the variable factor of human judgment on the part of the historian. Sir W. R. Wilde has emphasized the point by saying, "Men are liars, stones are not."

The materials employed in outfitting the grasping hand of man have been principally stone, particularly flint, quartz, and

obsidian; horn, bone, and ivory; metals; and wood. Of these substances wood is least enduring and so furnishes very little evidence today of the uses to which, in all probability, it was formerly put by prehistoric man. Of the metals copper, which occurs in comparatively pure form in nature, was first to be subjected to the use of man, while malleable bronze, an alloy of copper and tin, was invented and utilized long before iron, "the great lever of civilization," was successfully smelted from the ore.

Antedating the days of metal, however, was a long period when stones of various kinds, particularly *flints,* were fashioned by man for different purposes.

A. The Cultural Ages

Archæologists speak of three successive ages of human culture based upon the materials employed in the manufacture of tools and weapons. They are the *Stone Age*, *Bronze Age*, and *Iron Age*. To them might be added a fourth, the *Steel Age*, in which we live today.

These Ages were not uniform in duration in different parts of the world. Egypt, for example, had already reached a high point in the Bronze Age at the time when Europe still lingered in the Stone Age of culture (Fig. 86), while in North America and Australia the Stone Age was in full swing when these countries were discovered by white men within recent historic times. The native Tasmanians, the last of whom is said to have died in 1877, had never advanced beyond the culture of the early Stone Age. Some races of man still living today, such as the Hottentots of Africa, Veddahs of Ceylon, Botacudos of Brazil, Andaman Islanders, Fuegans, and Esquimaux, are still in a very primitive stage of tool culture.

B. The Evolution of Stone Handiwork

The Stone Age offers a most fascinating field for study since it furnishes the earliest direct evidence of human activity upon the earth.

The stone instruments of primitive man were fitted to various uses and included arrow-points, lance-heads, knives, axes, hammers, saws, choppers, borers, etchers, scrapers, and polishers, while one of the commonest types of flints was a generalized form to be grasped in the clenched hand, perhaps to add weight to an argumentative fist.

After 1838, when M. Boucher de Perthes discovered the first known ancient flint hatchet in a sand bed near Abbeville, France, together with rhinoceros and mammoth bones, a very great number of flint tools and implements of different degrees of perfection

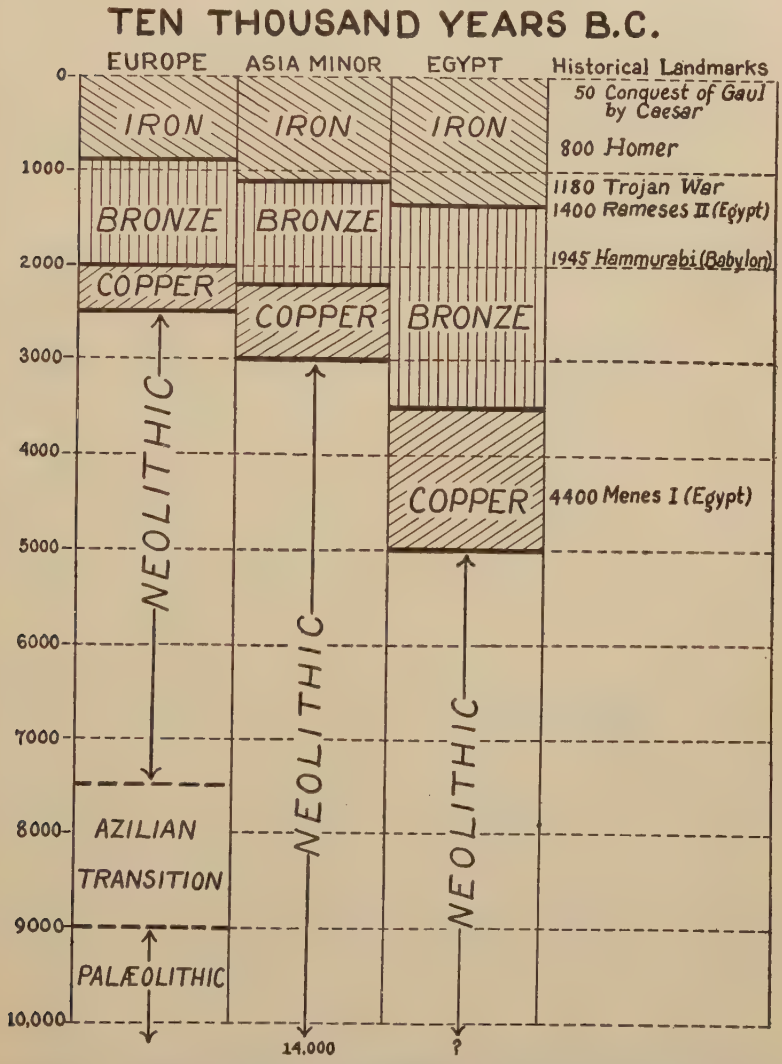


FIG. 86.—A chart to show that "cultural ages," while following the same sequence in different regions, were not of equal duration. (Modified from Boule.)

in workmanship, have been found and carefully studied. France has been particularly fortunate, not only in these records of early man but also in distinguished scholars who have collected and described them.

According to prescientific interpretations, relics of the Stone Age, chiefly flints, were described under the name of "fairy darts" and "thunderbolts," and their origin variously assigned to the devil, Druids, or Romans, a convenient trinity which has been made responsible for many other strange things.

Fig. 87.—Flints, representing three periods of the Stone Age. (Drawn from specimens in the collection at Brown University.)

Wherever fashioned flints have been found, even in such diverse regions as the Nile Valley, Algeria, Europe, England, America, and Somaliland, they exhibit the same universal patterns, and a parallel succession of evolutionary differences or degrees of refinement. It is thus possible to subdivide the Stone Age into three unequal divisions, namely, *Neolithic*, *Palæolithic*, and *Eolithic*.

The oldest type of stone implements, representing the Eolithic culture, are termed *eoliths* (Fig. 87). They mark the "great extent of time that has elapsed between the picking up of the first stones with an intelligent purpose, and the acquirement of sufficient knowledge to shape them into the crudest form of palæoliths" (Wilder). Eoliths, nowhere abundant, are always more or less problematical objects, since they are not undeniable artifacts in the sense of purposeful manufacture, but are merely pieces of stone of convenient size and shape to fit the hand, which, however, *show the effects of use*. Professor G. F. Scott Elliot says of them, "Surely if there is little to prove that coliths were made by man,

there is even less to convince us that they were formed in any other way." Reid Mohr, in 1910, described from a Pliocene "Red Crag" deposit in England certain doubtful "rostro-carinate" eoliths of peculiar but characteristic uniform shape which, if they were ever in prehistoric human hands, belonged to a type of man considerably more ancient than any that has left fossil remains.

The flints of the Palæolithic Period, as contrasted with the perhaps accidentally scarred eoliths, are unmistakably the result of human manipulation. They are all definitely chipped and fashioned (Fig. 87), and exhibit an evolution of workmanship from crude forms of early Palæolithic days, imperfectly chipped to the exquisitely fashioned instruments of later time in the "Golden Age" of the grotto painters. The palæolithic division of the Stone Age has been divided by experts into several periods, marking the successive advances in the art of chipping flints which reached the greatest excellence in workmanship with the Solutrèan Period. The names of these divisions are for the most part derived from the towns in France near which the characteristic flints were first discovered. Reading downward from the most recent to the most ancient, they are as follows:

Upper Palæolithic	*Azilian*, Poor workmanship. Decline of the art.
	Magdelenian, Bone, horn, and ivory employed.
	Solutrèan; Thin, laurel-leaf lance-heads, beautifully chipped.
	Aurignacian, Bone and ivory harpoons and needles.
Lower Palæolithic	*Mousterian*, Chipped on one side only.
	Acheulian, Sharpened to a point.
	Chellean, Oval, coarse chipping.
	Pre-Chellean, Hand wedges, chipped at one end only.

The stone tools of the comparatively short *Neolithic Period* are distinguished from those of the Palæolithic not only by being fashioned into definite shapes for obvious uses, but also by being *polished smooth* (Fig. 87).

Many flint instruments, particularly those of the Neolithic type, continued to be manufactured and used long after metals were employed in the Bronze and Iron Ages.

IX. TIME SCALES

There is no doubt that, to our myopic vision at least, the events of our individual lifetime are the most exciting part of all human history. But a single life of even "three score years and ten" is

only one one-hundredth of the approximate time involved in written history. Historical events that seem very ancient in contrast with the times in which we now live, appear quite recent against the background of the "Cultural Ages" of the archæologist, while the Cultural Ages in turn move magically forward into the present when their position in geologic time is considered. It is a good thing, however, occasionally to stretch one's sense of time by probing the abysmal past.

The following table is an attempt to visualize the relation of the reaches of time involved with respect to comprehensible historic units of time.

TIME SCALE

(Based on the unit in which a lifetime, or "three score years and ten," is equal to one minute)

	MINUTES AGO	HOURS AGO	DAYS AGO	YEARS AGO
A lifetime	1			70
Columbus discovers America	6			436
Christian Era begins	27½			1,928
Written history begins	100	1⅔		7,000
Cro-Magnon	430	7		30,000
Neanderthal	1,000	16⅔		70,000
Piltdown	2,000	36	1½	150,000
Heidelberg	3,500	60	2½	250,000
Pithecanthropus	7,000	120	5	500,000
Beginning of Cenozoic Era	42,000	700	30	3,000,000
Beginning of Mesozoic Era	130,000	2,100	90	9,000,000
Beginning of Palæozoic Era	260,000	4,200	180	18,000,000

X. CONCLUSIONS

The continuing wonder of mankind is man, for he is the most astonishing animal that ever lived on this earth. His achievements are like a rapidly widening wedge, and awaken "undiminished interest in every man born into the world" (Huxley). The fascinating theme of the anthropologist and the archæologist is particularly liable, however, to fall a prey to premature generalizations. Nevertheless certain conclusions from "spade history," as contrasted with legendary or written history, may be stated with considerable confidence.

(1) There are many converging lines of evidence which point unmistakably to the great antiquity of man when measured by any historical time scale.

(2) Man appeared in Europe in a remote time when the climatic conditions were different than at present, and when he was the contemporary of many kinds of animals now extinct.

(3) In America the evidences of human antiquity as yet discovered by no means go back as far as they do in Europe and Asia.

(4) The cradle-land of man was probably Asia. This continent is centrally located and distinguished by possible migratory routes connecting it with the other great land masses. Its vast size allows for a varying range of physical and climatic conditions that, in Tertiary times, might have made possible the emergence of human fore-runners from arboreal to land life. Moreover, Asia is known to be the ancestral home of most of the domesticated animals and of the oldest known civilizations.

(5) The direct descent of man is not through any of the kinds of living lemurs, monkeys, or apes. All modern primates, including man, are probably divergent offshoots from a common arboreal ancestor of very remote ancestry.

CHAPTER VI

UNITS OF STRUCTURE (CYTOLOGY)

I. THE CELL THEORY

It is quite essential in any house of knowledge to know the units out of which the intellectual edifice is built. Thus, the chemist must know the elements from which his compounds are made, the writer must be acquainted with the alphabet, the mathematician with numerals, and the biologist must know the units which combine to form the infinite diversity of living bodies.

The structural units with which the biologist deals are termed *cells*, and the science of cells is called *Cytology*.

Robert Hooke first suggested the word "cell" in 1665 when he described "little boxes or cells distinguished from one another" that he saw in thin slices of cork. The word, which suggests prison walls, is not a fortunate choice, however, for walls alone do not adequately describe the biological unit. Nevertheless it has come to stay and its use has now been extended to indicate all units of biological structure, regardless of whether the *walls* of a typical cell are in evidence or not.

The conception that all living structures are made up of organic units, or cells, dates from 1838–1839, when Schleiden and Schwann, botanist and zoölogist respectively, published important investigations upon the subject. The essential conclusions of the "cell theory," as now modified, are:

(1) Every living thing is composed of organic units (cells), or of the products of their activity.
(2) Every living thing begins life as a single cell.
(3) Every cell is derived by the process of division from some preceding cell.

II. A TYPICAL CELL

A generalized undifferentiated cell is represented diagrammatically in Fig. 88.

Near the center of the cell is the *nucleus*, surrounded by the *nuclear membrane*. Outside the nucleus is the *cytosome*, or body of the cell, enclosed in a *cell wall*, or membrane. Within the cytosome itself may be embedded various things, such as pigment granules, crystals, oil droplets, vacuoles, plastids, etc., and frequently there may also be identified in the cytosome a tiny body, the *centrosome*, from which radiate delicate lines in every direction. The nucleus is regarded as headquarters of the whole organized unit, since the changes which the cell undergoes seem to be initiated there. It is made up of more than one substance, a fact that is revealed by applying certain stains which, through chemical union, affect a part but not the whole of the nuclear substance.

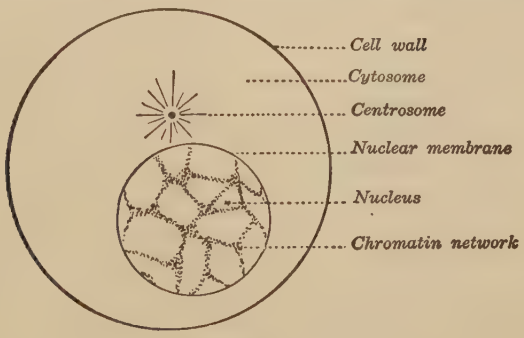


FIG. 88.—Diagram of a typical cell.

The part most easily stained is called *chromatin*, that is, "colored material." During certain phases of cell life the chromatin masses together into visibly definite structures, or bodies, termed *chromosomes*.

When cells mass together in the formation of tissues and become subjected to mutual pressure, the typical spherical shape becomes modified, and any of the several parts of the cell may undergo extreme modification, but most of the features outlined above, which make a cell an organized unit of living substance, characterize every cell.

III. CYTOMORPHOSIS

Cells are subject to the inevitable laws of change common to living things generally. The succession of changes through which each individual cell passes during its lifetime, is termed *cytomorphosis*. The term may be extended to include also the transfor-

mations through which successive generations of cells pass in the process of differentiation. Thus, according to Lewis and Stöhr,[1] "Cytomorphosis is a comparative term for the structural modifications which cells, or successive generations of cells, undergo from their origin to their final dissolution. In the course of their transformation, cells divide repeatedly, but the new cells begin development where the parent cells left off."

The initial phase of cytomorphosis is characterized by a lack of specialization. This is followed by a series of progressive changes in which the cell becomes finally fitted for its life work, whatever it may be. After a varying period of usefulness, signs of old age appear, and eventually the cell goes the way of all flesh and dies and its dead remains are removed from the society of its fellows. Some kinds of cells, like red blood corpuscles or epidermal cells, live a strenuous life, completing their entire cytomorphosis in a comparatively brief time, while others, like germ cells, may remain dormant for years in an undifferentiated, embryonic condition before they finally move forward to fulfill their destiny. Again, to illustrate the extension of the idea of cytomorphosis to successive generations of cells, as well as to the life history of an individual cell, the germinal epithelium of the *tubuli contorti* of the testis may be cited, which begins as simple epithelium and eventuates as differentiated spermatozoa.

There is much similarity between the life of a cell and of an individual. Both begin with a primitive, generalized stage; both pass through expanding infancy and differentiating youth; both arrive at specialized maturity and usefulness; both wear out and die. In one particular, however, there is a striking difference. The *individual* reproduces its successors only after it has become mature, that is, after it has differentiated or specialized. The *cell*, on the other hand, reproduces its kind only while still in the undifferentiated, embryonic phase, and it loses almost entirely the power to do this after it has attained specialization. The result is that certain cell units of the body, for example, nerve cells, when they have once gone through to the extreme end phases of their differentiation, have lost the power to replace themselves with daughter cells. They have passed beyond the embryonic stage of cytomorphosis in which replacement is possible, and then when they wear out they are unable to leave successors.

[1] *Histology*, p. 9.

IV. CELL DIFFERENTIATION

The path of specialization which a cell follows in cytomorphosis is dependent upon the work it has to perform in the cell community of which it is a part. The typical primitive cell, uncrowded by neighbors, tends to be spherical in form, but rarely has opportunity to remain so. *Red blood cells* of the lower vertebrates perhaps come nearest to retaining the original form of

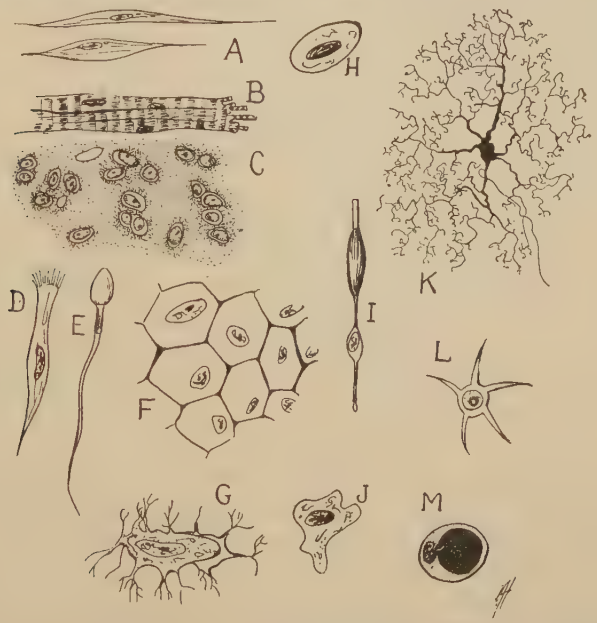


FIG. 89.—Various types of cells. *A*, smooth muscle cells; *B*, striated muscle cells; *C*, cartilage cells; *D*, ciliated epithelium; *E*, spermatozoan; *F*, squamous epithelium; *G*, bone cell; *H*, amphibian red blood cell; *I*, rod cell of retina; *J*, ameboid leucocyte; *K*, nerve cell; *L*, sperm cell of crab; *M*, fat cell.

embryonic cells, because the work they have to do of rolling about through the blood channels of the body, is facilitated by the spherical or ovoid shape. *Leucocytes*, or white blood cells, on the other hand, become irregular or ameboid in form, with the power of changing their shape, so that they are enabled to squeeze between the cells that form the walls of the capillaries, and thus escape out of the blood channels proper into the surrounding tissues, where they nose their way between other cells in their

sanitary mission of removing dead cells and devouring invading bacteria. *Squamous epithelial cells,* whose business it is to cover surfaces, become flattened like shingles, while *muscle cells,* which specialize in contraction, assume the much elongated form in which contraction is best accomplished. Certain detached cells, like *spermatozoa,* which need to acquire the ability to travel in a fluid without having the propelling power of the heart back of them, as the blood cells do, differentiate from their embryonic, spherical form into a tadpole-like shape with a powerful locomotor tail that effectually drives them forward about their business. *Skeletal cells,* the mission of which is support or protection, develop interstitial substance, while some *secreting cells* exhaust themselves in an excessive specialization of the cytoplasm, which is the consequence of their activity. Extreme modification of form is seen particularly in *nerve cells,* with their enormously attenuated processes, where specialization has gone so far that it is hopeless to expect them ever to perform any other function than that of long distance transmission. These examples of differentiation are only a few of the many guises in which the building blocks of organic structure appear. Some of these types of cell form are indicated in Fig. 89.

V. THE CHROMOSOMES

With the development of the compound microscope, the invention and utilization of aniline dyes, and improved cytological technique generally, the presence of chromosomes within the cell nuclei became known. The far-reaching importance of these peculiar structures has now been unquestionably established.

It has been found (1) that chromosomes are probably constant in numbers in all the various cells of every individual of any particular species of animals or plants; (2) that they behave in a predictable way throughout all the vicissitudes of cytomorphosis; (3) that not only every cell comes from a preceding cell, but that every chromosome in the nucleus comes directly from a preceding chromosome like itself, and (4) that when chromosomes, during the changes of cytomorphosis, break up into indefinite masses, thus apparently losing their characteristic shapes, they later reappear in the identical size and shape that they formerly had, which is evidence that their individuality is maintained

and that they are not simply chance masses of unorganized stuff. Not only do the various chromosomes of any cell assume characteristic shapes and sizes, but they occur *in pairs of two of each kind in every cell* (*autosomes*, Fig. 90).

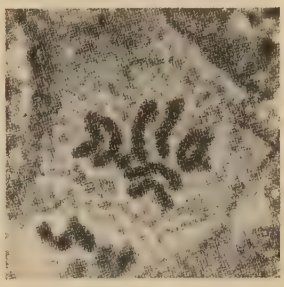


Fig. 90. — Spermatogonial chromosome group in a fly, *Dasyllis sp.*, showing autosomes associated in pairs, and the small x-chromosome (sex) without a mate. (From microphotograph by Metz.)

VI. MITOSIS

The usual behavior of the cell when two cells form out of one, is called *mitosis*. Although the astonishing details of mitosis are unknown and strange to the uninitiated, yet the process itself is occurring continuously in all living creatures, with countless repetitions. Upon its orderly action depends every step that serves to differentiate any animal or plant, starting at the fertilized egg and including all growth and organic repairs. The founders of the cell theory surely could not have dreamed of the extent of the vistas which their generalizations were destined to open up, for mitosis is a far more detailed and complicated performance than simply pinching the original cell in two.

The essential thing in cell division seems to be the equipping of each new cell unit with a set of chromosomes in its nucleus duplicating in number, form, and size those of the cell from which it came. Accordingly, in the process of cell formation, which consists of a parent cell dividing into two daughter cells, the chromosomes play the leading part. A very brief and general description of the phases of typical mitosis, with a series of explanatory diagrams, follows, but it should be remembered that the stages described as distinct really merge into each other continuously, like a moving picture, and that the actual process of mitosis will have taken place somewhere within the bodily structure of the reader many times over during the studious reading of this paragraph.

Four phases are recognized as sufficiently distinct to mark well defined changes from the "resting cell." These are known as the *prophase*, *metaphase*, *anaphase*, and *telophase*. The *resting cell* (Fig. 91, A) is characterized by the nuclear membrane,

a chromatin network within the nucleus, and sometimes by a centrosome. In the *beginning of the prophase* (Fig. 91, B) the centrosome has divided into two parts, while in the *early prophase* (Fig. 91, C) the two newly formed centrosomes have moved apart, and definite separate chromosomes have formed out of the chromatin network. The *prophase proper* (Fig. 91, D) is marked

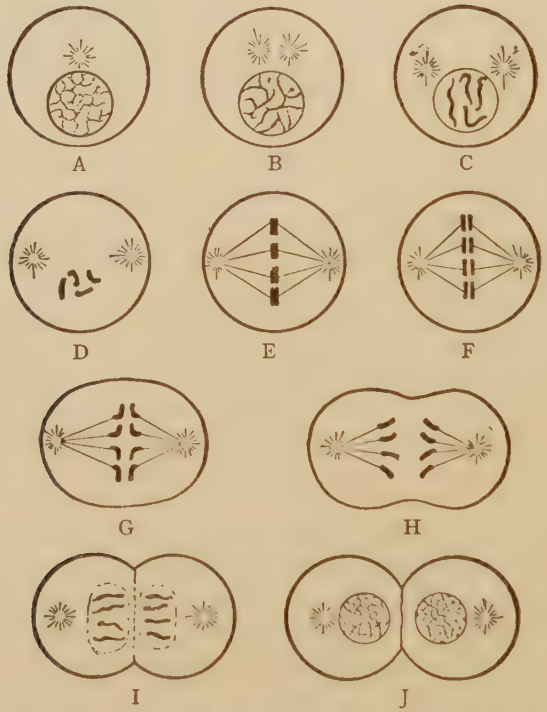


FIG. 91.—Mitosis diagrams. *A*, the resting cell; *B*, beginning prophase; *C*, early prophase; *D*, prophase; *E*, end of prophase; *F*, metaphase; *G*, beginning anaphase; *H*, anaphase; *I*, beginning telophase; *J*, end of telophase. (After Boveri.)

by the vanishing of the nuclear membrane. At the *end of the prophase* (Fig. 91, E) the chromosomes have come to lie at the equator of the cell, being connected by the mantle fibers with the centrosomes, each of which has now come to occupy a polar position. In the *metaphase* (Fig. 91, F) the chromosomes split lengthwise, and at the *beginning of the anaphase* (Fig. 91, G) these new chromosomes begin to separate from each other and

to move toward the poles, while the mantle fibers shorten. During the *anaphase* (Fig. 91, H) the cell body lengthens and begins to divide, while the migration of the chromosomes toward the poles is completed. In the *beginning of the telophase* (Fig. 91, I) the division of the cell body into two parts becomes complete. The mantle fibers have disappeared and the nuclear membrane begins to re-form around the chromosomes. Finally, at the *end of the telophase* (Fig. 91, J) the nuclear membrane becomes complete, the chromosomes break up into a chromatin network, and two resting cells take the place of the single one with which the process began.

VII. REPRODUCTION

Mitosis makes clear how cells are derived from preceding cells. It also indicates the process involved in the derivation of one individual from another by so-called asexual methods, whereby a fragment of an organism enlarges into a new individual. This is really nothing but another instance of growth wherein an additional part breaks free from the parent organism and establishes an independent individuality. It does not account, however, for the process of reproduction involved in the formation of a new individual from two parents.

Sexual reproduction, which is the prevailing means of increase in numbers among higher animals and plants, involves something more than an unbroken succession of mitoses. The essential feature of sexual reproduction is the combination of the chromosomal resources of two cells (egg and sperm) to form a starting point for a new series of mitoses.

If mitosis is making *two cells out of one*, then sexual reproduction is making *one cell* (*fertilized egg*) *out of two* (Fig. 92). As has been shown, mitosis is an elaborate mechanism whereby the *same number* of chromosomes is maintained throughout all the successive generations of cells that make up the individuals of any particular species. However, when cells from two such individuals unite in sexual reproduction, some provision must be made for the reduction of their chromosomes, or the cells of the new series of mitoses, resulting in a new individual, will have double the number of chromosomes typical for the species. This is accomplished by a preparatory process whereby half the chromosome material in each is discarded. This process

is termed *maturation*, or the reduction of the germ cell chromosomes. When the prepared, that is "mature," germ cells, each with half the normal equipment of chromosomes, join forces, the fertilized egg resulting has a complete orthodox outfit of

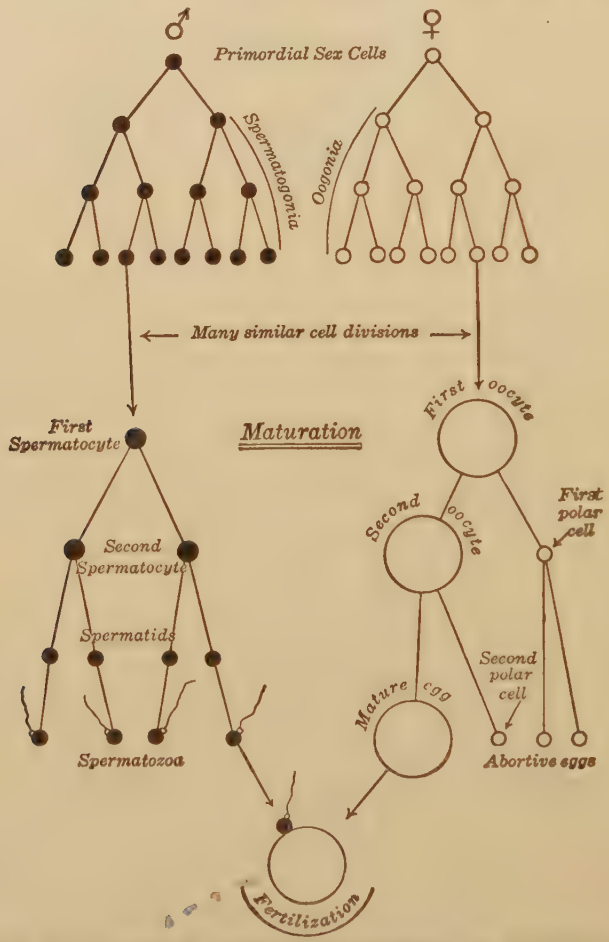


FIG. 92.—Diagram to show typical maturation and fertilization.

paired chromosomes, and thus the chromosome number remains constant throughout all the generations of the species in question. This also explains why the chromosomes in every cell, whatever their number, appear in pairs, because one of each kind comes from each parent.

VIII. THE DETERMINATION OF SEX

There is one outstanding exception to the rule that all individuals of any particular species have the same number of chromosomes in every one of their structural units. Among many animals there proves to be one more chromosome in each cell of the female than of the male, although curiously in birds as well as in butterflies and moths (Lepidoptera) the reverse is true, the male showing one more chromosome than the female in each component cell.

This difference in chromosome count occurs because *in one sex only* among all the pairs of mated chromosomes (*autosomes*) there is an odd chromosome without a mate. This odd chromosome is called the *sex chromosome*, since it is involved in the determination of sex (Fig. 90).

In man there are twenty-three pairs of "autosomes" in each cell, and in addition *in the male* a mismated pair of chromosomes, *x* and *y*, making a total of forty-eight chromosomes, while *in the female* besides twenty-three pairs of autosomes there is a pair of sex chromosomes, both *x*, likewise making a total of forty-eight. As a result of this inequality, when the sex cells undergo maturation and discard half of their equipment of chromosomes, the mature eggs are all alike (23+x), while the mature sperm cells are of two sorts, (23+x) and (23+y), according to whether the unmated *y* chromosome is rejected or not. The sex of the future individual is consequently determined by the kind of sperm that unites with an egg, as follows:

Egg	Sperm	Fertilized egg	
(23 + x)	+ (23 + x)	= (46 + 2x) =	♀ (female)
(23 + x)	+ (23 + y)	= (46 + xy) =	♂ (male)

Sometimes sex chromosomes, instead of being represented in one sex by a mismated pair, are present in one sex as an odd chromosome. In this case they are called the *x*- and *o*-chromosomes. The determination of sex, however, comes out exactly as in the odd chromosome case, that is:

Egg	Sperm	Fertilized egg	
(Autosomes+x)	+ (Autosomes+x)	= (Double autosomes+2x) =	♀ (female)
(Autosomes+x)	+ (Autosomes+o)	= (Double autosomes+1x) =	♂ (male)

Still other combinations of sex chromosomes have been observed, but although the number of autosomes varies in differ-

ent species of animals and plants, all cases agree in producing either *one kind* of mature eggs and *two kinds* of mature sperm, or the reverse, so that the determination of sex is always referable to a definite combination of the chromosomes, making the chances fifty to fifty that either sex results, which agrees approximately with observed findings.

IX. A WORLD OF BILLIONS

The total number of cellular units that takes part in the structure of a human body is beyond imagination. Dr. W. W. Keen, the eminent surgeon, has pointed out, for example, that the blood of a normal man weighing 144 lbs. equals about twelve pints, and that the total number of red blood cells per pint is computed at 10,240,000,000,000. Bierfreund estimates that a loss of three pints of blood may be made good in four weeks. This involves the manufacture of red blood cells at the rate of 45,000,000,000 per hour, or 760,000,000 per minute.

Dr. Keen further notes that the hair of a man's beard grows one millimeter in twenty-four hours. The constituent cells in the make-up of a millimeter of hair are, by count and computation over 10,000, so that seven or eight new cells per minute grow continuously for every hair. Multiplying this number by the total number of hairs of the head, one arrives at figures that are comprehensible only to an expert. The instances given concern but two of the many kinds of organic units which take part in making the human frame. When it is remembered that each one of these cells arises from a preceding cell by the elaborate machinery of mitosis, the laziest man may feel assured that he has accomplished something at the close of any day.

CHAPTER VII

DIVISION OF LABOR IN TISSUES (HISTOLOGY)

I. TISSUES

The science that deals with tissues, that is, *Histology*, includes Cytology that was considered in the preceding chapter. The cells, which are formed by successive mitoses, from the fertilized egg, or ovum, differentiate into various tissues that constitute the body. A tissue is generally an association of similar cells which have undergone specialization for some particular purpose. Thus bone tissue is made up of bone cells that are very much alike, and epithelial tissue is an association of epithelial cells that resemble each other.

The similar cells constituting a tissue may be connected with each other either by delicate strands of cytoplasm that penetrate the enclosing cell membranes, or by an intercellular ground substance of some sort either secreted by the cells themselves in the form of exaggerated cell walls, or formed out of intruded interstitial material arising extraneously.

Combinations of tissues occur in *organs* in much the same way that different textiles are combined into garments, and in turn organs together make *systems*, just as different garments together make costumes. For example, the stomach is an organ that is assembled out of muscle tissue, blood tissue, gland tissue, and other tissues, which together with other organs like the teeth, intestine, and pancreas, form the *digestive system*.

For purposes of description tissues may be classified as follows:

I. Fluid tissues.
II. Stationary tissues.
  1. Epithelial.
  2. Connective.
  3. Muscle.
  4. Nerve.

II. FLUID TISSUES

The fluid tissues are blood and lymph. Their cellular components are disconnected and are, therefore, constantly rearranging themselves with reference to each other, unlike the cells of

other tissues which maintain a comparatively stable spacial relationship with each other.

In the lower invertebrates, such as the cœlenterates and flatworms, the "blood" has no cells. In the higher invertebrates, and the lowest vertebrates (amphioxus), only ameboid white blood cells are present. The blood of all other vertebrates, is characterized by both white and red blood cells, and is consequently an elaborated fluid tissue.

Fluid tissues permeate the spaces which separate other tissues, and even the interstices between the cells of these tissues. They also occupy larger spaces, like the cavities of the joints, for example, and particularly circulate through special channels, called blood and lymph vessels, that extend to almost every part of the body. A further consideration of the blood is postponed until a later chapter.

III. EPITHELIAL TISSUES

Epithelial tissues (Fig. 93), are the most primitive of all tissues. They come in contact with other stationary tissues on one surface only, since they clothe the outer surfaces of the body and line various cavities and passages, including the blood channels. They also receive stimuli from the outside world, secrete and excrete different substances, and give rise to the highly important sex cells. There is usually a minimum amount of intercellular material in epithelial tissues. The cells composing them may assume a squamous, cubical, or columnar form, and may be arranged in more than one layer.

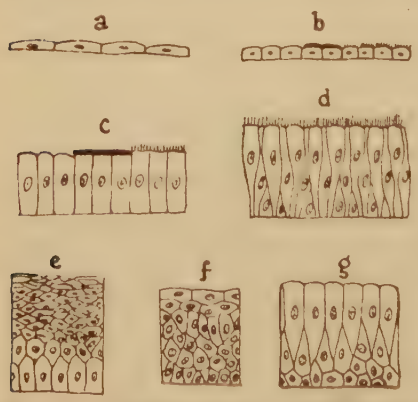


Fig. 93.—Epithelial tissues. *a*, one-layered flat epithelium; *b*, one-layered cubical epithelium, two cells with cuticle and four with cilia; *c*, cylindrical epithelium; *d*, ciliated epithelium; *e*, many-layered epithelium; *f*, transitional epithelium; *g*, stratified epithelium. (After Szymonowicz.)

In the same epithelium may sometimes be found differentiated cells modified for a variety of uses. For example, sense receptors together with their non-sensitive, supporting, cellular

companions, as well as gland cells, are found wedged between the typical cells of epithelial tissue.

The epithelial *glandular* tissues have a great variety of functions in the economy of the organism, namely, *digestive* in the salivary, gastric, and pancreatic glands; *defensive* in the poison glands of snakes, stink glands of skunks and other carnivores; *protective* in the mucous glands of fishes and amphibians, the shell-producing glands of molluscs, and the ink glands of squids; *lubricative* in the oil glands of the hair, and in mucous glands generally; *nutritive* in the mammary glands, and the albuminous and yolk-forming glands of birds; *constructive* in the spin glands of spiders and cocoon-forming insects; *cleansing* in the lacrimal glands of the eyeball; and *temperature-regulating* in the sweat glands of the mammalian skin.

When the substances produced by gland cells are utilized for the benefit of the whole organism, they are defined as *secreting* glands, but if the substances produced are waste products that are cast out of the body, they are termed *excreting* glands. If glands are supplied with a duct whereby their products may reach the outside or be poured into some cavity or passage-way, they are termed *exocrine* glands, but if no duct is present and the products of glandular activity must be transferred to the blood stream in order to be distributed, then they are known as *endocrine* glands, and the substances which they produce, as *hormones*. The morphology and behavior of the various glands will receive more attention later. It is sufficient now to assign them to their proper place among the epithelial tissues.

IV. CONNECTIVE AND SUPPORTING TISSUES

Connective and supporting tissues of vertebrates lie inside the body. The component cells of these tissues do not form layers, as epithelial tissues tend to do, but are massed together with more irregularity, and their intercellular substances are usually much more in evidence, particularly in cartilage and bone.

1. Connective Tissues

Included among connective tissues, whose mission is filling space between organs and parts of organs, are at least five different sorts that may, in some instances, merge into each other. These are

(a) gelatinous; (b) notochordal; (c) reticular; (d) adipose; and (e) fibrillar.

A. Gelatinous Tissue

Gelatinous tissue reaches its most characteristic development in sponges, and semi-transparent pelagic animals, like medusæ and ctenophores, in which the jelly-like bulk of the body is composed of secreted intercellular substance throughout which are scattered a few ameboid cells, frequently joined together in a very open meshwork by delicate cytoplasmic bridges. This type of tissue does not commonly appear in the bodies of adult vertebrates, although during embryonic development the so-called *mesenchyme* passes through a gelatinous tissue phase.

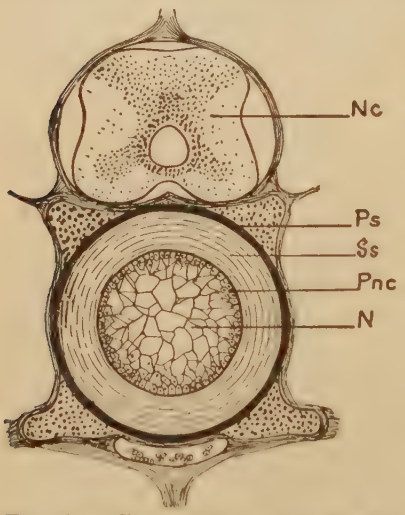


Fig. 94.—Cross section through the notochord and its sheaths, from a young dogfish. *Nc*, nerve cord; *Ps*, primary sheath; *Ss*, secondary sheath; *Pnc*, peripheral notochordal cells; *N*, notochord. (Drawn by K. L. Burdon.)

B. Notochordal Tissue

In notochordal tissue, on the contrary, there is a great reduction of intercellular material, so that the thin-walled cells lie closely pressed together (Fig. 94). Whatever rigidity is attained by this tissue is due principally to the fact that the cells are so tightly packed within a tough, containing sheath that a certain amount of turgor results, as when sausage meat is crowded into a casing.

Fig. 95.—Reticular connective tissue from a lymph gland of a cat, to show the supportive skeleton of a soft organ. (After Krause-Schmahl.)

C. Reticular Tissue

Reticular connective tissues (Fig. 95), form the meshlike supports that characterize many of the softer organs, like the spleen

and the lymph nodes, which are ordinarily thought of as being without internal skeletal devices of any kind.

D. Adipose Tissue

Adipose tissue is somewhat similar to the ordinary reticular tissue that forms the skeletal matrix of soft parts, for in this tissue also, groups of cells that specialize in fat storage lie enmeshed in a loose reticulum. When the fat cells are melted out of fat pork by frying, for example, a residual network is left behind which is the skeletal, or reticular, part of adipose tissue.

E. Fibrillar Tissue

Like other connective tissues, fibrillar tissue (Fig. 96) consists of cells but it is characterized principally by the fibers that interlace among the cells. These fibers, themselves the products of cells, are of two sorts, made up of white, non-elastic fibrils, and yellow, elastic fibrils.

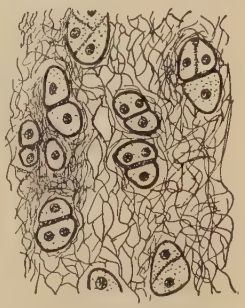


Fig. 96.—Fibrillar tissue in the form of elastic cartilage from the external ear of man. (After Böhm, Davidoff and Huber.)

The yellow fibrils are peculiar to vertebrates, not being found among invertebrate tissues. They occur in such parts of the body as the walls of blood vessels, the valves of the heart, the lining of the alveolæ of the lungs, and in certain intervertebral ligaments. Both the yellow and white fibrils may be compacted densely together, as in muscle sheaths, perichondrium, and periosteum; or they may be arranged in the form of a looser texture, as in the walls of blood vessels and the dermal part of the mammalian skin. In the sclera of the eyeball and in tendons, the fibrils are mostly white.

Fibrillar tissue plays an indispensable part in holding together nerves and muscles, muscles and bones, and in the transport of blood tissues. It is perhaps the most widespread tissue in the vertebrate body.

2. Supporting Tissues

A. Cartilage

Cartilage, or "gristle," is a non-porous, nerveless, bloodless tissue that enters into the skeleton of vertebrates. Its texture is not as firm and unyielding as bone, and consequently it is

better adapted as scaffolding, in water animals, such as fishes, where the surrounding medium helps to support the body, than for such use in land animals whose weight is held up in thin air.

There may be distinguished at least five kinds of cartilage, namely, (a) precartilage; (b) hyaline; (c) fibrous; (d) elastic; and (e) calcified.

Precartilage is a temporary embryonic type that precedes the formation of other kinds, but may sometimes endure in the adult organism, as in the fin rays of certain fishes. It consists of cells which have the power to secrete a thickened cell wall, or intercellular matrix, at the expense of their own cytoplasm. When this process has continued until the diminishing cells have isolated themselves from their neighbors in a sea of surrounding matrix, which is semi-transparent and somewhat firm, the *hyaline* stage has been reached (Fig. 97). Hyaline cartilage is found in the bendable and projecting region of the human nose, at the ends of the ribs joining the breastbone, in the stiff incomplete rings that keep the tracheal and bronchial tubes from collapsing, and in other parts of the body structure.

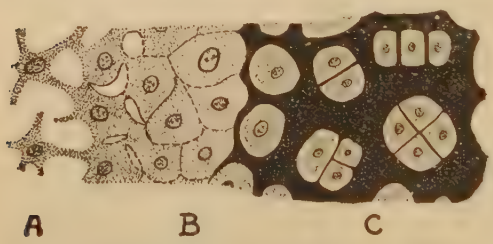


Fig. 97.—The differentiation of hyaline cartilage. *A*, mesenchyme cells; *B*, pre-cartilage; *C*, hyaline cartilage, with the hyaline matrix represented in black, in which the cells are embedded. (After Lewis and Stöhr.)

The hyaline matrix between the cartilage cells may be interwoven with fibers, either white or yellow, as in fibrillar connective tissue, in which case either *fibrous*, or *elastic* cartilage is the result. Fibrous cartilage is typically seen in the padlike discs separating the centra of the vertebræ in the backbone, while elastic cartilage is found, for example, in the epiglottis, and in the framework of the external ear, which fortunately, as a result, springs readily back into its original shape when bent. Sometimes the intercellular matrix of hyaline cartilage becomes infiltrated with limy salts, when it is designated as *calcified* cartilage.

B. Bone

Bone is the most conspicuous of the skeletal tissues of vertebrates. As contrasted with cartilage, it is porous and supplied

with nerves and blood vessels, and is considerably more rigid. It includes at least two kinds of cells, *osteoblasts* and *osteoclasts*. The first of these are *bone-forming* cells, which produce the limy intercellular matrix that characterizes bone. The osteoclasts, on the other hand, are *bone-wrecking* cells, which tear down bone tissue and make possible the rearrangement of material necessary to the accomplishment of growth among such unyielding building materials as bone cells.

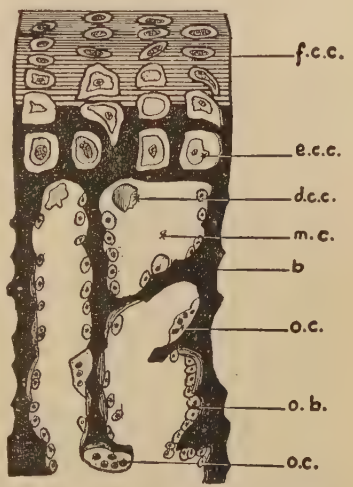


FIG. 98.—The formation of bone. *f.c.c.*, flattened cartilage cell; *e.c.c.*, enlarged cartilage cell; *d.c.c.*, degenerating cartilage cell; *m.c.*, marrow cavity; *b*, bone; *o.c.*, osteoclast; *o.b.*, osteoblast. (Modified from Klein.)

Bone consists of two essential substances, first, an organic base of living cells, and second, in the excessively developed matrix surrounding these cells, an infiltrated mass of inorganic, limy salts. These two components are so intimately united that there is no visual way of separating them, yet each alone is sufficient to give characteristic shape to a bone, for when the organic part is burned out by fire, or the inorganic component is dissolved away by acid, the part remaining in each instance preserves the original form of the bone.

In relative weight the inorganic or mineral part of bone is about three fourths of the whole, although the ratio of inorganic to organic varies with age, ordinarily becoming greater the longer the bone lives. According to Heintz an analysis of the mineral constituents of a human femur resulted as follows:

Calcium carbonate	9.06%
Calcium phosphate	85.62%
Magnesium phosphate	1.75%
Calcium fluoride	3.57%
	100.00%

Embryonically active cells, *osteoblasts* (Fig. 98), are responsible for the formation of bone tissue. By their rapid multiplication

living bone cells are formed, which in turn secrete the *lamellæ*, or hard parts. As bone grows, however, it becomes necessary not only to add new tissue but actually to remove that which has already been formed. For example, when one compares the lower jaw of an infant with that of an adult (Fig. 99), it is evident that no single cell of the former structure can persist unchanged throughout the process of growth. The jaw of an infant is not simply added to as it becomes larger, but all the building material composing it must be broken down bit by bit and reassembled and supplemented many times before the adult bone is formed. It is as if a stone wall were enlarged not simply by adding to the outside of it as it stands, but by tearing it down and reassembling it with additional stones so as to enclose a larger area.

Fig. 99.—Diagram comparing the jaw of an infant with that of an adult. (After Kölliker.)

This wrecking of bone tissue already formed, in order to make way for rearrangement and enlargement, is accomplished by rather large definitely identified cells, called *osteoclasts*. The destructive work of these cells is not always followed by constructive reorganization, however, for when the work of the osteoclasts exceeds that of the osteoblasts, a bone decreases in size. Thus in toothless old age, (Fig. 100) not only the lower jaw becomes smaller through the loss of teeth but also the bony sockets in which the teeth were set decrease in size through the removal of tissue by the osteoclasts, so that the chin and the nose tend to hobnob together (Fig. 101).

Fig. 100.—The condition of the jaw in old age, showing the acute projection of the chin resulting from the loss of teeth and the absorption of the sockets for the teeth.

Some bones of the body, particularly those of the roof of the skull, are formed by osteoblasts directly, while others, notably those that make up most of the skeleton, are at first laid down in cartilage. This temporary cartilaginous scaffolding becomes later invaded by an army of destructive osteoclasts (more properly

chondrioclasts), which are followed up by constructive hosts of osteoblasts, transported to the scene of reorganization from outside the area in question, with the result that the cartilage is bit by bit replaced by bone

When a slice of bone, taken, for instance, from a cross section through the shaft of the femur and ground down to translucent thinness, is examined under the microscope, it is seen to be made up of innumerable small plates, or *lamellæ*, (Fig. 102). These plates are of inorganic material and are arranged in more or less orderly fashion with reference to the minute spaces which they enclose, in at least three general ways, concentrically, interstitially, and circumferentially.

FIG. 101. — In toothless old age the chin and the nose tend to hobnob together. (After Camper.)

The *concentric lamellæ*, somewhat like the rings of growth around the pith of a shrub, envelop small tubelike, branching canals, the *Haversian canals*, which permeate the bone lengthwise and are the conduits for the passage throughout the bony tissue of capillaries, lymphatics, and nerves. The Haversian canals, surrounded by the concentric lamellæ, are

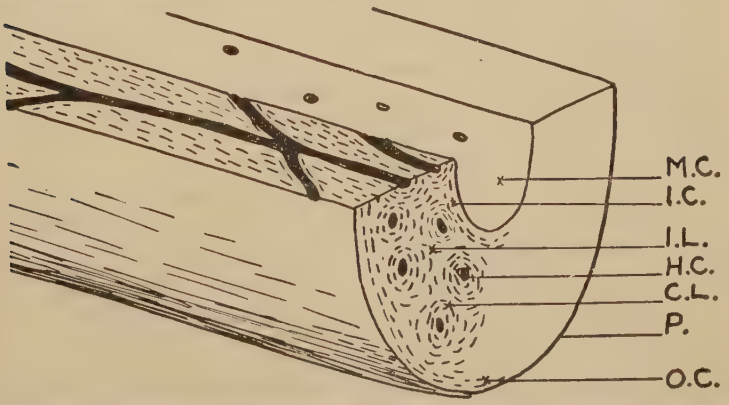


FIG. 102.—A diagrammatic stereogram of bony tissue. *Haversian canals* and *lacunæ* in black, leaving the bony *lamellæ* white. *M.C.*, marrow cavity; *I.C.*, inner circumferential lamellæ; *I.L.*, interstitial lamellæ between the Haversian systems; *H.C.*, Haversian canal; *C.L.*, concentric lamellæ surrounding an Haversian canal; *P.*, periosteum, or skinlike connective tissue enveloping the whole bone; *O.C.*, outer circumferential lamellæ.

most typically seen in the dense tissue of the cylindrical shafts of the long bones in the appendages, where they communicate both

with the periosteal coverings of the bone on the outside and also through the entire bony tissue to the marrow cavity inside. They constitute the highways for organic traffic throughout the bony tissues, making this part of the skeleton a living adjustable structure.

The necessarily irregular *interstitial lamellæ* fill up the spaces between neighboring Haversian systems, and finally, the *circumferential lamellæ* either run around the entire bone like a cortex, on the outside just beneath the periosteum, or as an internal layer, grade over into the spongy tissue that borders the marrow cavity within the bone.

FIG. 103.—A diagram showing a fragment of bone tissue at the edge of an Haversian canal, through which blood vessels and nerves penetrate the substance of the bone. Eight lacunæ, each containing a bone cell, are indicated, and also their connection by *canaliculi*. The bony lamellæ are represented in black.

The Haversian canals are not the only spaces, however, that help to make the living bone porous. Between the hard lamellæ, separating them from each other, are tiny spaces, *lacunæ*, literally "little lakes," in which lie imprisoned the living bone cells themselves. Lacunal spaces communicate with each other through microscopic holes in the walls of the limy lamellæ, called *canaliculi*. The relation of these structural details is shown in Fig. 103.

C. Teeth

The teeth of vertebrates are among the most enduring of animal tissues. The *dentine*, or ivory, that makes up the bulk of a tooth, surrounds the *pulp cavity* which houses the nerve supply and the nutrient blood vessels, but is not itself traversed by nerves or capillaries although it is honeycombed by very minute parallel canals. Usually the exposed surface of a tooth is faced with *enamel*, the very hardest of all tissues, which is prismatic in structure and entirely without minute canals. In those teeth which are set in sockets the roots are embedded in *cement*, a bonelike tissue that anchors the tooth firmly to the jaw.

V. MUSCLE TISSUE

One of the commonest manifestations of life is movement. Even in stationary plants living cytoplasm streams about within the cells, and fluids are passed from one part to another.

Within the animal body certain members of the cell community, like blood cells, shift about with much freedom, while other kinds of cells, leucocytes for example, are able to change their shapes. The well-nigh universal ability of living cells to move or to change shape, culminates in *muscle cells*, whose conspicuous contractility not only causes internal movement but exercises an influence for motion in more or less distant parts of the body to which they are directly or indirectly attached. The cytoplasm of the elongated muscle cells is differentiated into *sarcoplasm* and *myofibrils*, and the accommodating sheath, an intrinsic part of the cell, which clothes the changeable sarcoplasm like a thin rubber glove, is termed *sarcolemma*. The myofibrils are embedded in the sarcoplasm and are the particular mechanism of elasticity. They are peculiar in that they effect contraction in only one direction instead of in any direction as is the case of ordinary contractile cytoplasm.

Muscular movement is always effected by the *pull* of muscles, while restorative movements are in turn brought about by the pull of antagonistic muscles, and not by the relaxation that follows contraction. Muscle tissue is thus simply specialized tissue in which the general functions of motion are carried out more effectually than elsewhere. Dr. A. E. Shipley has vividly emphasized the power that may be stored in muscle tissue by citing the performance of a jumping flea. Someone succeeded in weighing nine fleas and found the average weight to be 0.38 mgm. These creatures leap from 8 to 13 inches. If a man, who weighs perhaps 70 kgms. made a corresponding leap he would go horizontally 36,000 miles, or once and a half times around the world.

There are three kinds of muscle tissue that differ in their degree or manner of specialization, namely, (1) smooth; (2) striated; and (3) cardiac.

1. Smooth Muscle Tissue

Smooth muscle cells with but a single nucleus near the center of the cell, are spindle-shaped and rarely forked at the ends.

In man they vary in size from 15 micra (15/1000 of a millimeter) in blood vessels, to 200 micra in the digestive tube, while in the walls of the uterus during pregnancy they may reach 600 micra in length. In the pliant walls of the bladder they are more or less felted together, lying in every direction, so that the bladder when it is emptied contracts like a toy balloon rather than collapsing like a hot-water bag.

Smooth muscle cells are rarely massed together into bulky tissues, being widely distributed throughout the body. For example, they are found in the skin, where they act as hair-raisers, feather-fluffers, and doorkeepers of glands, while they also form a part of the contractile walls of various passage-ways, such as blood and lymph vessels, the digestive tube (except the upper part of the esophagus), the trachea and bronchi, the reproductive ducts, and ureters.

2. Striated Muscle Tissue

This tissue is "flesh," and in man it constitutes nearly fifty per cent of the weight of the entire body. It is found not only in the bulky body wall and the muscles of the limbs, where it effects locomotion, but also, in the higher vertebrates at least, in the diaphragm, tongue, esophagus, pharynx, larynx, and the muscles of the eyeball.

The component fibers of striated muscle tissue are enormously elongated, so that a single nucleus is no longer able to serve so extended a territory. In consequence many nuclei, like substations, are scattered along the fiber just beneath the sarcolemma, instead of in the central portion, as is the case with smooth muscle. The descriptive term "striated" means that the myofibrils, which extend throughout the long diameter of the cells, are differentiated into alternate bands, that not only refract the light differently and stain differently with aniline dyes, since they vary *physically* and *chemically*, but also behave differently upon contraction, showing that they are *physiologically* different too. The dark, or *anisotropic bands*, are doubly refractive in polarized light, and shorten upon contraction more than the light colored, or *isotropic bands*, which are singly refractive in polarized light. Since these alternate bands are alike in extent and match each other side by side in the parallel myofibrils, they cause a striated appearance across the entire muscle cell. In birds the "white meat" of the

breast is characterized by an excess of myofibrils, while the "dark meat" has more sarcoplasm and less myofibrillar substance.

In general the striated muscles effect quick movements of comparatively short duration and are *voluntary*, that is, under the control of the will, while smooth muscle tissue is *involuntary* and much slower in action. There are some notable exceptions to this generalization, for the body muscles of certain molluscs are smooth and voluntary, while the visceral muscles of insects and crustaceans are typically striated and involuntary.

3. Cardiac Muscle Tissue

The tissue of the muscular heart is transitional in character between smooth and striated, in that the component cells are comparatively short, branching, and involuntary in action, although striated in appearance and multinucleated (Fig. 104). The enormous dynamic force exercised by any kind of muscle tissue is seldom realized. The tireless heart of a man, for instance, knows no rest, as one ordinarily thinks of rest, and throbs faithfully without skipping a beat throughout a long lifetime.

FIG. 104.—Cardiac muscle cells. (After Szymonovicz.)

VI. NERVE TISSUE

Nerve tissue is characteristic of animals rather than of plants, although the nervous function of sensitivity is a fundamental property of cytoplasm and is by no means absent from plant life. It consists of specialized nerve cells, or *neurones*, accompanied by nutritive components of various sorts, connective tissue, and non-nervous *neuroglia cells* of ectodermal origin. The cytoplasm of neurones is differentiated into *neuroplasm* and *neurofibrils* which differ in their chemical composition, as shown by staining methods. Neurofibrils are particularly fitted for the reception and transmission of impulses, just as myofibrils are the specialized instruments of contractility in muscle cells.

The typical shape of neurones represents extreme modification from their characteristic spherical embryonic form, the cytoplasm being drawn out into extremely elongated processes, or fibers, of two kinds, called respectively *dendrites* and *neurites* or *neuraxons*. Dendrites are numerous and branch freely, as their name indicates, while there is only one neurite to each cell. This neurite may be

insulated from surrounding cells by a fatty envelope, known as the *medullary sheath*, outside of which it, in turn, may also be enclosed in a connective-tissue covering of cellular origin, called *Schwann's sheath*. The dendrites are usually without either of these sheaths. When impulses travel through a neurone along the neurofibrils, they do not go at random, but always enter through some one of the dendrites and pass out through the neurite. Impulses are relayed from cell to cell by contact between the neurite of one cell and the dendrite, or cell body, of the next.

"Nerves" are bundles of neurites outside the central nervous system, and are enclosed in a common connective sheath, while *ganglia* are aggregates of cell bodies of neurones clustered together, for regulation and correlation of impulses. Nervous tissue thus accomplishes a double mission, first, that of relating the organism to its environment through the sense organs, which are made up of sensory receptors of the various stimuli and secondary components which support and nourish the neuronic receptors; and second, that of regulating and correlating all activities by means of the central and sympathetic nervous systems.

Professor G. H. Parker refers[1] to the human cerebral cortex, in connection with the matter of memory, as a "superficial layer of the brain with a thickness varying from one and a half to five millimeters and covering an average of 2,352 square centimeters. This cortex is estimated to weigh about 658 grammes. It is composed chiefly of blood vessels, supporting tissues, and nerve cells. The blood vessels and supporting tissues are merely mechanical accompaniments of an apparatus the real functions of which are carried on by the nerve cells. These cells have been carefully studied, their arrangement and distribution made out, and it is estimated that in a single cortex their number is not far from 9,200,000,000. Notwithstanding this prodigious number, these cells and their processes represent only two per cent of the total weight of the cortex; in other words, the cortical nerve cells and their processes in the average man weigh about thirteen grammes. This amount represents a little less than a cubic inch of material or about one five-thousandth of his total weight."

Dr. Parker concludes with the following impressive words: "By means of it we cherish the traditions of the past; its activities include all our conscious states, our simple sensations, desires,

[1] *Biology and Social Problems*, p. 37, Houghton, Mifflin Co., 1914.

hopes and aspirations, our sense of shame and regret at deeds of unworthiness, our joy in generous acts, our knowledge of all these things; from it emanate the impulses to those steps which mark us as honest or dishonest, extravagant or thrifty, secretive and deceptive, or frank, open and free, cold or affectionate, in short all those signs which stand for personality. Socially no part of our bodies is more precious than this cubic inch of cortex. From the cradle to the grave we work to train it. Our early childish plays and lessons are intended to awaken it into activity. The school, the college, the university work upon it; our whole educational system is devised to bring into full efficiency this cubic inch of our body. It must be enriched by experience; it must be trained to make wise decisions, to call forth acts of friendly service. If you have any doubts of the enormous social significance of this cubic inch of nervous tissue, look upon the individual in which it permanently breaks down, a useless member of society, a charge upon the state, if not upon the race."

CHAPTER VIII

THE DEVELOPMENT OF THE INDIVIDUAL (EMBRYOLOGY)

I. THE STARTING POINT

No animal or plant is an orphan in the sense that it is without parentage. The spontaneous origin, even of the most minute organisms, at least under present conditions on this globe, has been effectually disproved. Modern control of bacterial diseases, together with the incalculable boon of aseptic surgery and antiseptic practice, depends upon the clear understanding of this fact. A new organism may be introduced into the brotherhood of living things by one parent or by two, but no animal or plant comes into the world of today unsponsored by preceding life.

When there is only one parent the new individual is said to arise by *asexual* reproduction. The method of *sexual* reproduction, however, which involves a double source, is by far the commoner way in which higher animals and plants begin their separate existence.

The starting point of a sexually produced individual may be regarded as a *fertilized egg*, which is a combination of contributions from two parents.

It is the purpose of this chapter to try to trace some of the more important episodes in the "miraculous pageant of transformations" that take place between the fertilized egg and the adult organism. This is the particular province of *Embryology*, and some familiarity with the fundamental concepts of this fascinating field in biology is essential to any comprehensive understanding of the structure and function of adult animals and plants.

II. THE NECESSARY PARTNERS

1. Differentiation of the Germ Cells

Two germ cells, the *sperm* and the *egg*, are necessary partners in the enterprise of a fertilized egg.

Fertilization is the union of two diverse germ cells, and consequently provision has to be made for getting them together.

The egg which must be stored with first-aid nutriment for the future organism during the critical early stages of its development, tends to become relatively heavy and stationary. The inevitable corollary of this differentiation in the egg is that the sperm must assume all the responsibility of travel in the necessary process of getting together. The egg does not meet the sperm half way. The sperm has to cover the entire distance.

The fact that different terms, namely, "pollen grains" and "ovules," are employed to designate the reproductive units in plants, does not indicate any essential differences in the germ cells of animals and plants.

2. Kinds of Sperm

The result of the physiological necessity of the union of two different kinds of germ cells, is that the sperm cells of animals and the pollen grains of plants, which carry the corresponding male germ cells of the higher plants, become specialized into structures adapted particularly for locomotion.

A typical sperm cell is pictured in Fig. 89, E, in which it is seen that the differentiated *head* of the sperm is principally made up of the original nucleus, carrying the important chromosomes that are freighted with hereditary determiners, while the *middle piece* and the locomotor *tail* represent transformed cytoplasm, modified for particular uses. An animal sperm is thus adapted for locomotion through a fluid medium by sculling forward by means of a vibratile tail. Animals never employ aërial routes for this purpose, as do plants, which may have their pollen grains borne to the egg cells located in the ovules of other flowers by the wind or the agency of insects.

Among vertebrates, most fishes and amphibians broadcast their eggs and sperms in water, and the sperm cells travel in this medium in order to reach the egg. Among land forms like reptiles, birds, and mammals, internal fertilization occurs, so that their sperm cells travel up the oviduct to the egg in a fluid medium that serves the same purpose as water in the case of aquatic animals. Copulation, which occurs with many land animals, is simply a device for insuring placement of locomotor sperm cells in a suitable highway leading to the waiting egg.

An exception to the almost universal type of sperm with a locomotor tail, is found among certain worms (*Ascaris*, for ex-

ample), and crabs where an ameboid or angular form is assumed by the sperm cell, and the approach to the egg is accomplished by much slower creeping movements or by direct contact upon rubbing together (Fig. 89, L).

3. Kinds of Eggs

Eggs of animals differ specifically in the load of nutritive yolk which they carry. Curiously those with a minimum amount of

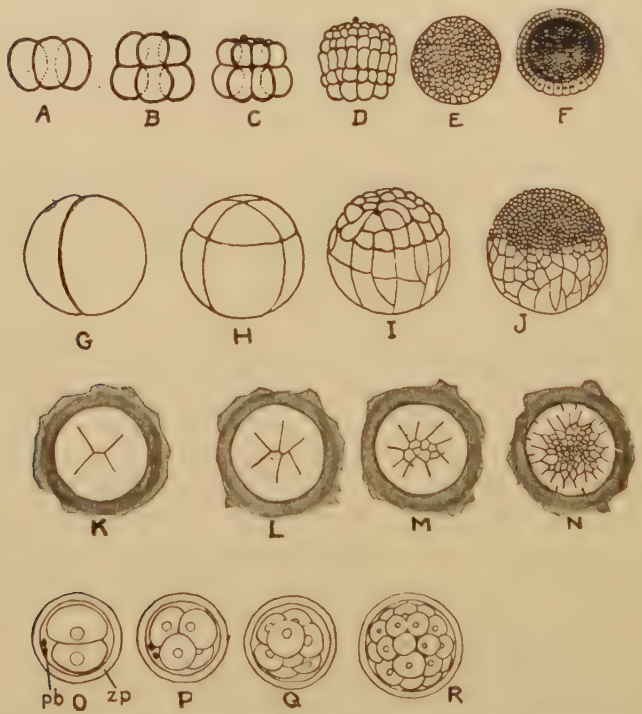


FIG. 105.—Stages in the segmentation of the egg. *A–F*, amphioxus. (After Hatschek.) *G–J*, Ambystoma. (After Eycleshcimer.) *K–N*, chick. (After Coste.) *O–R*, rabbit. (After van Beneden.) *p.b*, polar bodies; *z.p*, zona pellucida.

yolk are found at the two extremes of the vertebrate scale, namely, the eggs of amphioxus and of mammals. The egg of amphioxus probably represents a primitive condition in the matter of acquisition of yolk, while the poverty of yolk in the egg of mammals is not due to primitiveness but has no doubt come about through a different chain of causes. These causes are correlated with the

fact that not much stored food is required in the eggs of this group, since they early become implanted like a parasite in the uterine wall of the mother from whom they derive their necessary nutritive start in life. As a consequence of the scarcity of yolk, the mammalian egg is remarkably small, that of man measuring only about 1/125 of an inch in diameter (Fig. 375).

In cyclostomes and amphibians the abundant yolk is massed particularly in the heavier, lower, or "vegetative," half of the egg (Fig. 105, G–J), while the nucleus and most of the cytoplasm, constituting the embryogenic, or "animal" pole, appear on the upper side. Such eggs may be described, therefore, as *polar* or *telolecithal eggs.*

In reptiles and birds (Fig. 105, K–N), there is so much yolk present that the essential nucleus of the egg cell, and its tiny halo of active cytoplasm, form only a small area, the *germinal disc.* The yolk invariably gravitates when unhindered, so that the disc comes to lie on the upper side of the relatively large sphere. In addition there is also a reserve food supply of nutritive albumen, or "white," packed around the egg itself within the protective shell (Fig. 377). If one stretches the point and regards a bird's egg with its auxiliary parts as a single cell, it must be allowed that it is the largest of all animal cells. Thus, the egg of the wingless *Apteryx* of the antipodes, weighs nearly one-fourth as much as the entire bird. An ostrich's egg is equivalent in bulk to about two dozen hen's eggs, while that of the extinct gigantic "moa" of New Zealand (Fig. 48), had twelve times the mass of an ostrich's egg and might, therefore, easily hold the palm as being the largest animal "cell" ever discovered.

III. CLEAVAGE

After the union of sperm and egg, the first of the long series of stages that transform the fertilized egg into an adult individual occurs, a process called *cleavage* (Fig. 105). This consists of a rapid succession of mitoses in which the initial cell becomes divided in turn into two, four, eight, and so on, until a mass of small cells results without appreciable increase in the total weight from that of the fertilized egg. These small cells, or units, are called *blastomeres*, each one of which contains a complete double set of chromosomes, bearing hereditary potentialities from two parents, thus duplicating the original outfit in the fertilized egg.

The purpose of these rapid preliminary cell divisions of cleavage seems to be to break up the original cell into many separate workable units, for a very fundamental principle underlying differentiation is *division of labor*, and this is facilitated when there are different nuclear centers present for the initiation of different cellular enterprises.

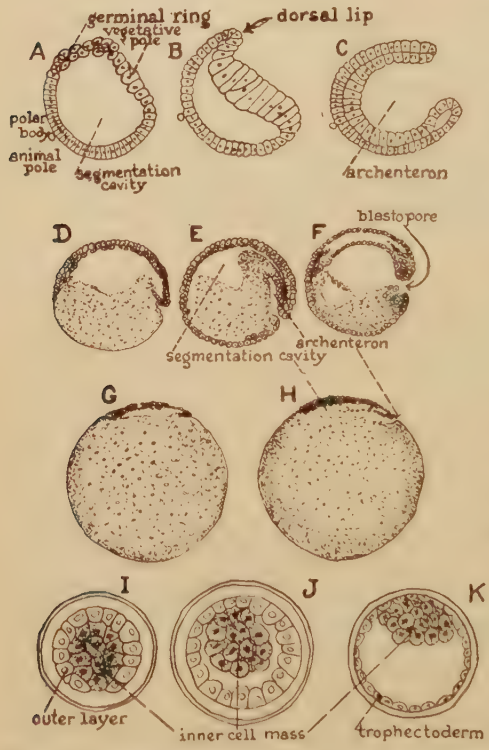


FIG. 106.—Gastrulation. In amphioxus. *A*, blastula showing flattening of the vegetative pole and rapid proliferation of cells in the postero-dorsal region; *B*, commencement of infolding of cells at the vegetative pole; *C*, invagination complete as the result of continued involution of the dorsal lip. (After Cerfontaine.) In frog, *D–F*; in chick, *G–H*. (After Hyman.) In rabbit, *I–K*. (After Keith.)

IV. THE BLASTULA

The results of cleavage are dependent upon the amount of inert yolk present. In amphioxus, where there is very little yolk to hinder the process of cell division, the entire egg mass is equally involved in cell formation, and the resulting blastomeres of essentially uniform size, arrange themselves in the form of a hollow sphere, called the *blastula*, while the cavity within is termed the *segmentation cavity* (Fig. 106, A).

When the yolk is disposed in polar fashion, as in an amphibian's egg (Fig. 105, G–J), the mitoses at the embryogenic or animal pole in the neighborhood of the original nucleus, go forward at an accelerated rate, while the cell division is retarded at the opposite pole, where the lifeless yolk is particularly in evidence. A blastula is evidently formed but the segmentation cavity within the hollow sphere is eccentric (Fig. 106, D), its walls are of very unequal thickness,

and the blastomeres at the embryogenic pole are considerably smaller and more active than those at the opposite or vegetative pole.

In reptiles and birds the results of segmentation are still further modified by the relatively enormous amount of yolk present. The nucleus of the fertilized egg undergoes the usual mitosis, but the new cell boundaries fail to be extended at once so as to include the great sphere of yolk material. The result is a patch of crowded blastomeres of unequal size at the embryogenic pole, the larger ones with incomplete boundaries being at the periphery (Fig. 105, M–N). This growing disc extends its margin until eventually the entire sphere of yolk is covered and enclosed by cells which gradually incorporate the underlying yolk mass within. The segmentation cavity is apparently suppressed, although a subgerminal cavity, present in the segmenting eggs of birds and filled with a fluid even in unfertilized eggs, is usually regarded as the "segmentation cavity." Meanwhile, at the blastogenic pole the body of the embryo itself has assumed definite form (Fig. 106, G–H).

The mammalian egg, in spite of its scarcity of yolk, does not behave in segmentation like primitive amphioxus, which it resembles in its small supply of yolk. The reason for this difference is probably that mammals have inherited developmental traditions from a series of ancestors which amphioxus never had. Mammalian cleavage resembles more that of reptiles and birds than any more primitive ancestors, although birds are obviously not in the direct line of mammalian descent. The entire egg is divided into blastomeres but without the regularity characteristic of amphioxus, and with the result that, instead of a hollow blastula, an irregular solid mass of cells is formed. Later the peripheral blastomeres of the germinal mass form a somewhat distinctive layer, enclosing more spherical central cells (Fig. 106, I–K). Fluid collects within this mass and a hollow sphere results, with the cells arranged in two kinds, an outer enveloping sort, the *trophectoderm*, which comes into contact with the inner wall of the uterus where the developing embryo becomes implanted, and an eccentric *inner cell mass*, which is destined to give rise to all the cells that are to take part directly in the formation of the embryo.

The "inner mass of cells" becomes further differentiated into

ectoderm, and *entoderm*, the latter enclosing a cavity that may be regarded as the *archenteric cavity*.

V. GASTRULATION

In the forms that produce a blastula, the cells at one pole of the hollow sphere divide oftener, and become more numerous and crowded than at the other pole. Since they remain in contact with each other without changing their relative positions to any great extent, they tend to form a continuous layer that is more than sufficient to make up the original surface of the sphere. They are therefore forced to find a new space to occupy, and this is accomplished by pushing into the segmentation cavity at the region of the more slowly growing vegetative pole with the result that a double cup, or *gastrula*, is formed (Fig. 106, C). The new cavity within the inner cup is termed the *archenteron*, and its opening to the exterior, the *blastopore*. These relations are very clearly seen in amphioxus but are somewhat obscured in the amphibian egg where the segmentation cavity is not surrounded by walls of equal thickness, and a relatively smaller archenteron comes to occupy an eccentric position (Fig. 106, E).

In reptiles and birds, before the disc of blastomeres has spread out to envelop the large yolk, there forms at its edge on one side a crescentic fold of tissue that pushes in under the margin of the disc and produces a potential cavity homologous to the archenteron of the lower vertebrates, whose eggs are less hampered with yolk (Fig. 106, H).

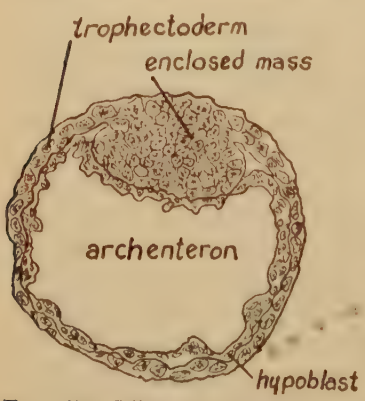


FIG. 107.—Bilamellar blastocyst of a mammal. (After van Beneden.)

The formation of the archenteron in the mammalian egg comes about as already indicated through the activity of the peripheral cells of the eccentric inner mass that projects into the segmentation cavity. These migrate out to form a layer lining the original fluid-filled cavity, which now becomes the archenteron (Fig. 107). As the result of gastrulation the cells are arranged in two layers. Those of the outer cup, facing the outside, form the *ectoderm*, and

those of the inner cup, surrounding the archenteron, the *entoderm*. The ectodermal cells are in a position to begin to assume the sensory functions of the nervous system, or, in the broad sense, mediation with the environment, while the entodermal cells, lining the primitive food canal or archenteron, take on nutritive activities.

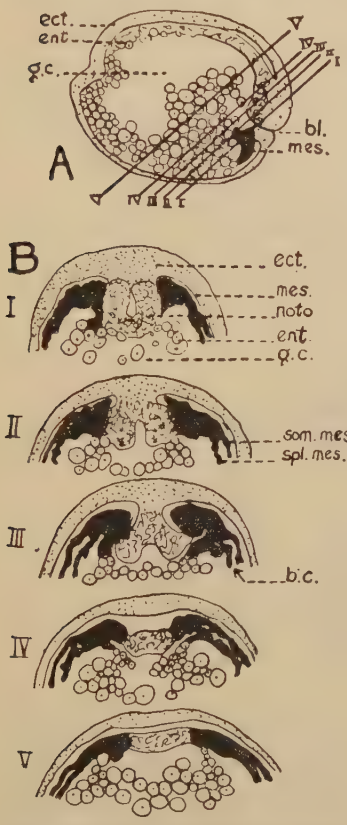


FIG. 108.—*A*, long section through an embryo of a newt, *Triton*. *B*, *I–V*, cross sections through the same embryo in the planes indicated in *A*. *bl.*, blastopore; *ect.*, ectoderm; *ent.*, entoderm; *g.c*, gastral cavity; *mes.*, mesoderm; *noto.*, notochord; *som.mes.*, somatic mesoderm; *spl.mes.*, splanchnic mesoderm; *b.c.*, body cavity. (From Schimkewitsch, after Eismond.)

VI. RISE OF THE MESODERM

At the critical junction between ectoderm and entoderm, within the compressed segmentation cavity (Fig. 108), the *mesoderm*, a new group of cells with great potentialities, is born. These new cells in vertebrates proliferate rapidly into the region that represents the former segmentation cavity which has become practically obliterated by the approximation of the ectodermal and entodermal walls.

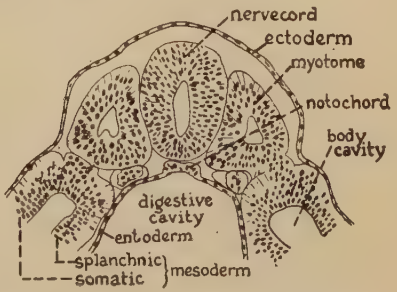


FIG. 109.—Transverse section of an embryo of 2.5 mm, showing on either side of the medullary canal a mesodermic somite (myotome), with the intermediate cell mass and ventral mesoderm. (After von Lenhossek.)

The mesoderm cells form a mass that soon splits apart to form

a new cavity, the *cœlomic cavity*, within the mesoderm itself. The result is that the mesoderm is separated into two regions of embryonic tissue, an outer layer, or the *somatic mesoderm*, next to the ectoderm, and an inner layer, the *splanchnic mesoderm*, next to the entoderm (Fig. 109). The cœlomic cavity thus formed, with a lining of mesodermal cells on all sides, gives rise to the future peritoneal cavity, and also, in the higher vertebrates, to the pericardial and pleural cavities. These general cavities in the adult are formed from numerous embryonic components.

In amphioxus, for example, the cœlomic cavity is formed rather as a series of independent paired sacs, or cœlomic pouches, arranged

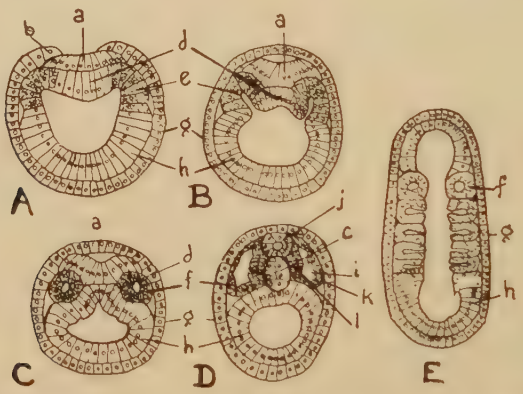


FIG. 110. —Formation of the neural tube, notochord, and mesoderm in amphioxus. *A–D*, cross sections; *E*, frontal section. *A*, differentiation of *a*, the medullary plate; *d*, the notochordal plate; *b*, the neural folds, and *e*, the mesodermal pouches. *B*, the neural folds have closed across above the medullary plate; the mesodermal pouches have evaginated somewhat; *C*, mesodermal pouches, *f*, have closed off from the entoderm; *D*, neural tube, *j*, and the notochord, *c*, and the somatic, *k*, and the splanchnic, *l*, mesoderm begin to be evident; *E*, segmentally arranged mesodermal pouches, *f*, appear. *a*, medullary plate; *b*, neural fold; *c*, notochord; *d*, notochordal plate; *e*, mesoderm; *f*, mesodermal pouches; *g*, ectoderm; *h*, entoderm; *i*, cœlome; *j*, neural tube; *k*, somatic mesoderm; *l*, splanchnic mesoderm. (From Parker and Haswell, after Hatschek.)

along either side of the long axis of the body (Fig. 110). As these sacs expand, their neighboring walls are pressed into direct contact with each other. Later the double transverse partitions thus established break down, and only the longitudinal double walls remain, forming the *mesenteries*, dorsal and ventral, that separate the long body cavity on the right side from that on the left side. Usually the ventral mesenteries also break down subsequently

(Fig. 111, H), bringing the cavities of the two sides into free communication with each other and leaving only the dorsal mesenteries. Between the thin approximated walls of the dorsal

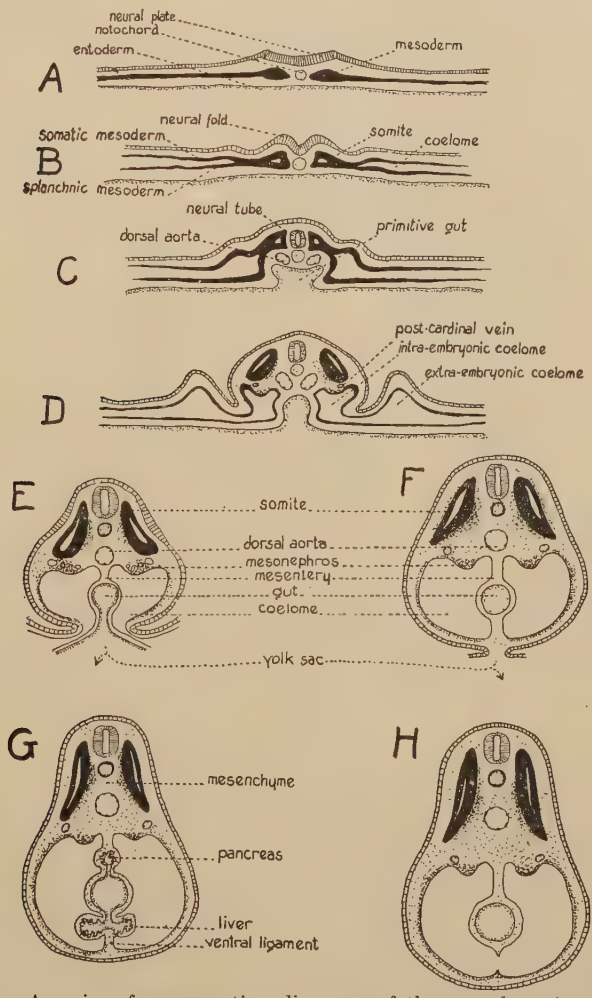


Fig. 111.—A series of cross-section diagrams of the mesoderm in the chick. (After Parker and Haswell.)

mesenteries, blood vessels and nerves may extend to and from the digestive tube.

In a cross section of a developing embryo (Fig. 112), it is possible to distinguish three general regions of mesoderm which are

different enough to warrant special descriptive terms. They are (a) the dorsal, or *epimeric* region, out of which most of the voluntary muscles of the body and much of the dermal layer of the skin develop; (b) the middle, or *mesomeric*, region, from which the excretory apparatus of the primitive kidneys comes; and (c) the ventral, or *hypomeric* region, that gives rise to mesenteries, peritoneum, the involuntary muscles of the digestive tube, and the gonads, which produce the germ cells.

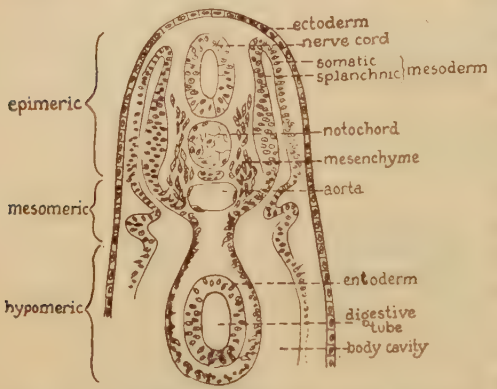


FIG. 112.—Diagrammatic cross section through a dogfish, showing cavity of the myotome still connected with the body cavity. Wandering mesenchyme cells are shown migrating from the mesoderm to occupy the spaces between somatic mesoderm and ectoderm on the one hand, and the splanchnic mesoderm and entoderm on the other. (After van Wijhe.)

In animals that arise from eggs loaded with an abundance of yolk, like the chick, the formation of the body cavity within the mesoderm does not result, as in amphioxus, from a fusion of a double row of cœlomic sacs. As already pointed out, the *germinal disc*, or nuclear headquarters of the fertilized egg, undergoes cleavage until a patch of blastomeres is formed on top of the big yolk. These pioneer cells and their descendants then set out to spread over and envelop the entire yolk. Those on the outside become the ectoderm, those underneath next the yolk itself, the entoderm, while between the ectoderm and the entoderm are the mesodermal cells.

As the mesoderm spreads towards the periphery, it splits into two layers, the somatic and splanchnic mesoderms, and the space thus formed between the two layers is the cœlomic cavity (Fig. 111, D). In this case, however, the cœlomic cavity on either side is a continuous space not formed by the fusion of separate cœlomic sacs, although a series of open pockets, suggesting cœlomic sacs, develops in the mesoderm, like stalls in a community garage, near the mid-dorsal line of the lengthening embryo. These are the *somites* of the epimeric region,

which are destined later to be transformed largely into body muscles.

In man, the formation of the early mesoderm is apparently somewhat different, being precociously formed as a layer inside the trophectoderm. The *inner cell mass* differentiates into two, in each of which a cavity appears by the confluence of intercellular spaces. The upper one is the *amnionic cavity*, lined by embryonic ectoderm, and the lower one is the *yolk sac*, lined

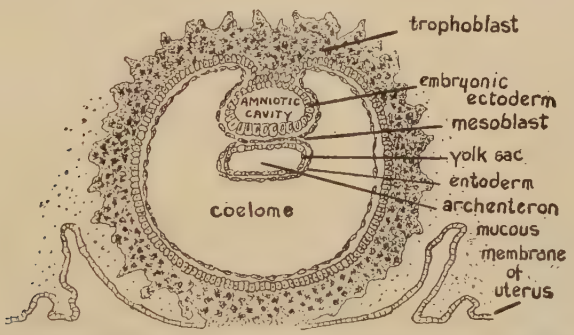


FIG. 113.—Showing the origin of the primitive cœlome, the mesoblast, and the cavity of the amnion, during the development of the human ovum. (From Keith, after T. H. Bryce.)

by entoderm (Fig. 113). The ectoderm and entoderm are still in contact at the region of the *primitive streak*, from which critical junction the later mesoderm, particularly that of the embryo itself, arises, much as in all other forms.

VII. EMIGRATION OF THE MESENCHYME

Early in the differentiation of the mesoderm, cells of a new sort, collectively known as the *mesenchyme* (Fig. 111, G, H), arise from the *outside* of the somatic mesoderm and the *inside* of the splanchnic mesoderm. These mesenchyme cells emigrate from the mesoderm layers and take possession of all the remaining chinks in the old, partially obliterated segmentation cavity. At first ameboid in shape and behavior, the mesenchyme cells, in the course of many cell generations, give rise to a considerable part of the body, including the skeletal and circulatory tissues. Thus, in a sense, the mesenchyme is the child of the mesoderm and the grandchild of the entoderm.

VIII. FORMATION OF THE NERVOUS SYSTEM

With gastrulation and the formation of the archenteron there begins to be an increase in size, or *growth*, accompanied by the differentiation and establishment of the organs and systems that constitute the mechanism of the adult animal. One of the earliest systems to become evident is the nervous system.

Along the dorsal side of the ectoderm the cells begin to multiply at a greater rate than in the surrounding region, thus forming a thickened band called the *neural plate*. The increased mitotic activity in these cells soon results in the formation of a groove along the neural plate as the cells push down into the underlying segmentation cavity, which is undergoing obliteration by the encroachment of the expanding entoderm. This furrow of ectodermal cells, the *medullary groove* (Fig. 114), is the fore-runner of the central nervous system. Eventually the medullary groove with its cellular walls is completely buried within the embryo. Its edges come together forming the hollow tube of the nerve cord, and it is pinched off entirely from the outside ectoderm from which it originated. This process of rapid inpushing growth, resulting in a hollow structure, is called *invagination*, and it is a good illustration of the far-reaching *principle of unequal growth* in the process of differentiation. In fact "unequal growth," unequal in quantity or rate, lies at the very foundation of many processes of morphogenesis, which constitute much of the subject matter of embryology.

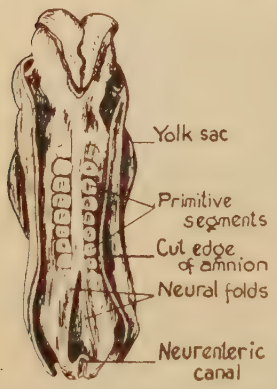


FIG. 114.—Dorsal view of human embryo of 2.11 mm. (Eternod), showing the neural folds still open. (After Arey.)

IX. ORIGIN OF THE NOTOCHORD

At about the time when the cœlomic cavity is forming by the splitting of the mesoderm into two layers, the longitudinal group of cells along the mid-dorsal line of the archenteron, at least in amphioxus, (Fig. 110, C), is pinched off from the entoderm and devoted to the formation of the *notochord*. In other

vertebrates the notochord is derived directly from cells in the region of the lip of the blastopore (Fig. 108).

Around the notochord as a core, the surrounding mesenchyme cells lay the foundations of the vertebral column. After the notochord is isolated from the dorsal wall of the archenteron, a tissue of *secondary entoderm*, or entoderm proper, remains, which is destined to form a major part of the lining of the digestive tube in the adult.

X. ASSEMBLING OF THE DIGESTIVE TUBE

While the ectoderm and mesoderm are assuming their respective rôles in the developing embryo, the entoderm, or lining of

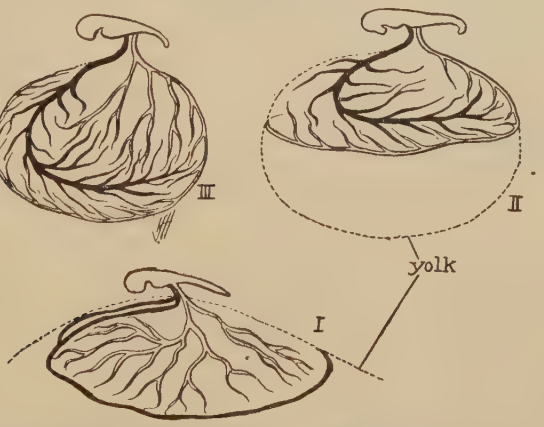


FIG. 115.—Three stages in the process of enveloping the yolk by embryonic blood vessels. (After von Lenhossek.)

the archenteron, gives rise to the notochord, having laid the foundation for the future digestive system as indicated in the preceding paragraph.

In those animals whose eggs are laden with yolk, the *yolk sac* forms by the encroachment of the spreading embryonic tissues which grow around and finally enclose the yolk (Fig. 115). The nutritive material in this sac thus has direct access by means of the vitelline, or yolk, blood vessels through the *yolk stalk* to the cells lining the archenteron, and in this primitive digestive cavity it is utilized by the rapidly differentiating embryo. As the content of the yolk sac diminishes, and the need for an arrangement whereby nutriment may be taken into the growing organ-

ism from the outside world becomes imminent, the *digestive tube* with an inlet at one end and an outlet at the other, is formed. The basis for this compound passage-way for food is that part of the archenteron which is lined with secondary entoderm after the notochord is pinched off. This cavity is supplemented at either end by invaginations of the ectoderm that finally break through from the outside into the cavity of the archenteron, thus forming a continuous canal. The inpushing of the ectoderm at the anterior end which marks the region of the mouth, is called the *stomodæum*, while the corresponding invagination at the posterior end, which forms the anal exit of the food tube, is called the *proctodæum* (Fig. 116). Thus it comes about that food passing through the alimentary tract first rubs against walls of ectodermal origin, then follows along a major distance in contact with entodermal walls where much of it is absorbed, and finally whatever remains passes out surrounded by ectodermal walls again.

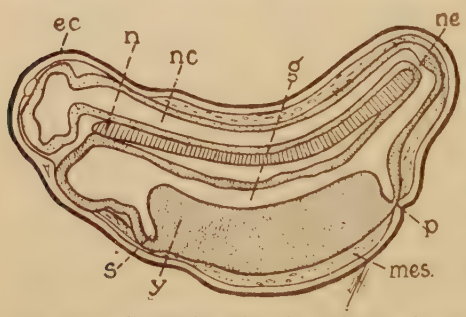


FIG. 116.—Sagittal section through a toad embryo. *ec*, ectoderm; *g*, gut; *mes.*, mesoderm; *n* notochord; *nc*, nerve cord; *ne*, neurenteric canal; *p*, proctodæum; *s*, stomadæum; *y*, yolk. The entoderm is stippled. (After Goette.)

At special points along the alimentary tube certain cells undergo particular differentiation in order to care for the enormous and diversified traffic that is destined to take place along this important highway. So arise in different vertebrates, lungs, liver, digestive glands of various sorts, swim bladder, crop, gizzard, cæcal appendages, and other derivatives of the digestive tube.

XI. THE MAJOR CAVITIES

With the passing of the segmentation cavity through the intrusion of the mesoderm and the mesenchyme and the incorporation of the archenteron into the digestive tract, the original cœlomic cavity, among the mammals at least, becomes divided into three different sorts of new spaces, namely, the

pericardial, the peritoneal and pleural cavities that serve to house different organs.

The cœlomic cavity becomes divided first by a double transverse mesodermal wall, the *transverse septum*, into an anterior and a posterior chamber. The former space develops into the *pericardial cavity* containing the heart, and the latter, into the *peritoneal cavity*, or "body cavity" proper, in which various organs come to lie. In mammals the mesoderm intrudes between the two walls of the transverse septum and helps to form a *muscular diaphragm*, that aids mechanically in the process of respiration. The transverse septum of some fishes does not entirely separate the pericardial from the peritoneal cavities, so that communication between the two persists throughout life in the form of the so-called *pericardio-peritoneal canal*.

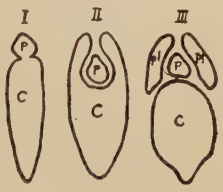
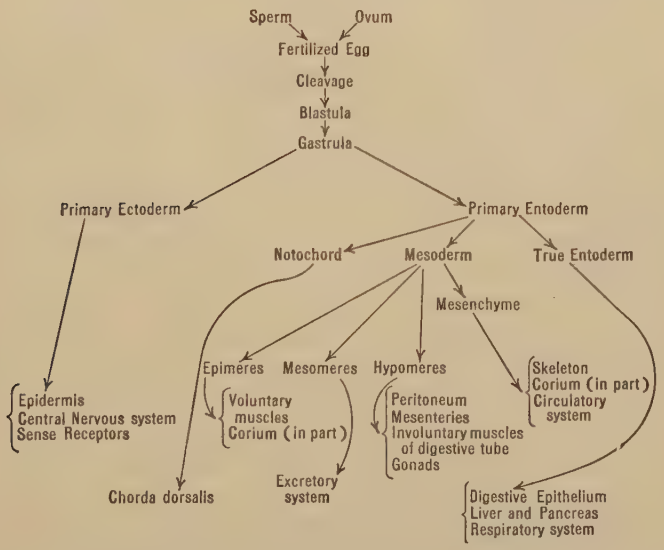


FIG. 117. — Diagrams of the evolution of the major cavities. *c*, cœlomic cavity; *p*, pericardial cavity; *pl*, pleural cavity. (After Gegenbaur.)

THE FATE OF THE GERM LAYERS



Second, there arises among mammals, in addition to the pericardial and peritoneal cavities an additional pair of anteriorly

placed cavities that come to lie on either side of the pericardium. They are the *pleural cavities* and contain the lungs. The double median wall formed by these two pleural sacs as they press against each other, is called the *mediastinum* (Fig. 117).

FIG. 118.—Outlines of early human embryos, natural size, from 25 to 120 days of age. (From Arey. The first six stages are after His; the last two, after DeLee.)

XII. THE FATE OF THE GERM LAYERS

It is now possible to review, in seven-league boots, the important steps by which the germ layers emerge from the fertilized egg, and to see in dim outline how these pregnant embryonic tissues give birth to the principal adult tissues and organs that make up the individual.

The table on page 163 indicates these steps, but within the confines of a single brief introductory chapter it is necessary to avoid the many alluring side alleys that entice the embryologist from the direct pathway, and to be content with only a fleeting glance at the oft repeated marvel of the development and differentiation of a fertilized egg into an adult individual.

Diagrams of the early stages in the development of the human embryo are shown in Fig. 118.

XIII. SOMA AND THE GERM LINE

In the long series of mitoses that follow the initial fertilized egg, there soon comes a time when the daughter cells resulting from some particular cell division are no longer identical twins. They may still have the same kind of chromosomal equipment as the result of the preceding mitosis, and may be indistinguishable in appearance, but, as their future behavior shows, they have come to a fundamental parting of the ways, for one of the pair is now destined to become the ancestor of the myriad cells that differentiate into various tissues and organs to form the growing individual (*soma*), while the other is fated to be the ancestor of all the succeeding eggs and sperms (*germ line*), and so to be charged with the necessary business of reproducing the species (Fig. 119).

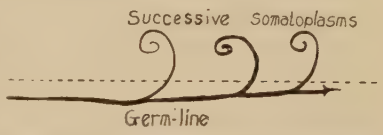


Fig. 119.—Diagram to show how the continuous germ line gives rise to successive somas, or individuals.

There are some pronounced differences in these two streams of differentiating cells. The soma becomes the conspicuous thing which is known as the animal or plant, and is biologically the guardian of the inconspicuous and less commonly known germ line. The soma is *mortal*, for after a time it inevitably breaks down and dies either a natural or a violent death. The germ cells, on the other hand, although they may perish with the dying soma, are *potentially immortal*, since they form the only biological bridge across which the spark of life may be borne from one generation to another in vertebrate animals.

It is quite possible to go backward in imagination step by step, without a break in the life line of living cells, from any individual cell of an adult organism to the fertilized egg from which it came, and to see how the material in that fertilized egg was in turn a

part of the unbroken series of germ cells that were housed in the preceding generations of somas, and so on to the very remotest ancestral source.

The soma, within limits, can maintain and repair itself. The germ line can not only do that but it can also give rise to new somas. This is its mission, to reproduce new individual organisms, while it is the business of the soma, or the individual, to nourish, protect, transport, and unite germ lines. Otherwise inevitable death ends all.

XIV. THE SUCCESSION OF GENERATIONS

The resemblance between individuals of successive generations, which is so conspicuously apparent everywhere, has its explanation

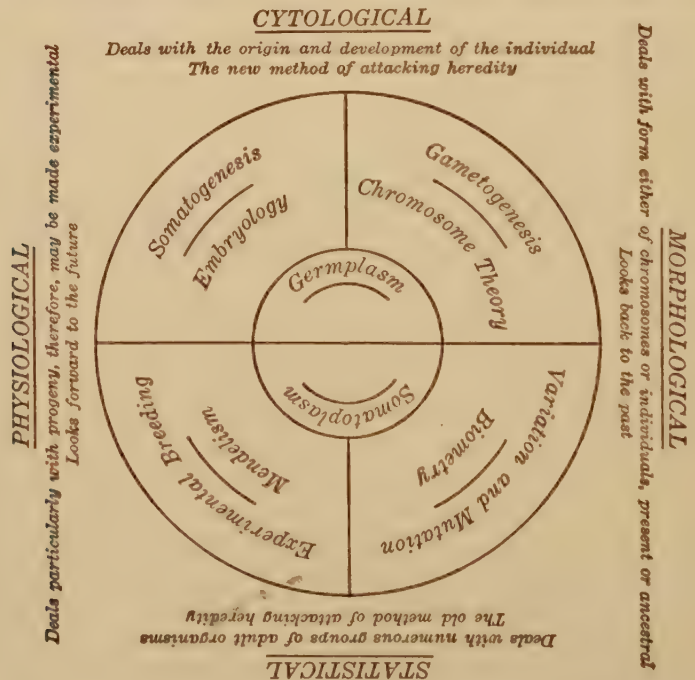


FIG. 120.—Any-side-up diagram of Genetical Sciences. (From the author's *Genetics*.)

in the fact that both parent and offspring are somatic expressions of the same stream of germplasm. That is why "pigs is pigs," and chickens hatch out of hens' eggs. The laws of heredity

(*Genetics*), are thus concerned fundamentally with the *behavior of the germ line*, and the expression of it in the soma.

There are various ways to get at the matter. In the past it has been done largely by comparing points of likeness and difference in individuals of succeeding generations of a species. This *somatic method* is facilitated by the experimental breeding of animals and plants. During the last quarter century great advance has been made by such breeding through applying the fundamental principle known as "Mendelism."

Another line of advance is the direct study of the germ line itself, which has given rise to an increasing army of biological specialists, who are concerned with the intimate behavior of chromosomes, particularly those of germ cells. To them we are indebted for an expanding body of knowledge about *spermatogenesis* and *oögenesis* in animals and plants, or the facts and laws which concern these germplasmal origins.

A diagrammatic representation of various approaches to the science of heredity is shown in Fig. 120.

CHAPTER IX

BIOLOGICAL DISCORDS (PATHOLOGY)

I. THE POINT OF VIEW

One of the chief concerns not only of medical practice and surgery but of daily life as well, is the repair of biological machinery that has gone wrong. There has been no lack in the past of guesses and traditions as to the *whence* and *why* of bodily ills, with the result that a vast store of misinformation and hearsay has accumulated along with the truth. This makes a happy hunting ground for "medicine men" and quacks, and is fertile soil for the production of cure-alls and "patent" medicines. One difficulty with the up-keep of the human machine is that, unlike an automobile, extra parts are not procurable, if false teeth and wooden legs are excepted.

The scientific study of the *causes* of biological discords (*Etiology*), is comparatively recent. In order to succeed in such investigations it is necessary to know what it is that has gone wrong, and this is the field of *Pathology*, which forms the basis of every system of medicine worthy of consideration. Pathology, or the study of the *abnormal*, goes hand in hand with *Physiology*, the science which deals with the *normal* activities of organisms. In fact it is highly important first to know the normal in order to understand the abnormal. Both physiology and pathology in turn depend upon a knowledge of *Morphology*, or the science of form and structure, for normal as well as abnormal function is almost always referable to a structural basis.

II. DEVIATIONS FROM THE NORMAL

The "normal" is the prevailing type. If nearly all house cats were of the tailless Manx variety, a cat with a tail would appear abnormal, just as the unusual condition of six-fingeredness is regarded as abnormal simply because most people have only five fingers, including the thumb, on each hand.

Deviations from the normal frequently turn out to be a handicap to their possessors. The very fact that normality is only

another way of saying that success has been gained in some particular by a *majority* of individuals, implies that variations from the standard have, in all probability, been less successful. Deviations, however, are not always unfortunate. Left-handedness, for example, is exceptional but is not necessarily a handicap. Deviations from the normal that do handicap the possessor may take the form of deformities, misplacements, or disturbances, external or internal, that work ill to the organism. *Disease* itself, which is the particular province of pathology, may be defined broadly as *any departure from the normal standard of structure or function of a tissue or organ.*

There are at least three elementary activities of organisms, namely, (1) *formative,* which result in the growth and establishment of structural parts; (2) *metabolic,* which have to do with the maintenance of the organism; and (3) *responsive,* which concern the interplay between the organism and the stimuli that affect it. Under normal conditions there is an optimum relation in each of these three lines of activity. An injury, or a disease, may upset this optimum balance and cause either a cessation of these activities (death), or a quantitative or qualitative modification of one or all of them.

III. DISTURBANCES THAT WORK ILL

1. Internal Disturbances

Disturbances that work ill to an organism by upsetting the optimum balance may be internal or external in their origin, although it is not always easy to determine to which of the two categories a particular case belongs.

Although an outline analysis might be carried to much greater length, only four kinds of probable internal disturbances will be mentioned, namely, (1) formative disturbances; (2) mechanical interferences; (3) responsive activities; and (4) hereditary handicaps.

A. Formative Activities

When the complicated activities of growth and differentiation, to which attention was called in Chapter VIII, are passed in review, one wonders that so few structural mistakes or accidents actually occur. The successful outcome of all embryonic development depends constantly upon the precise timing and infallible performance of each step, because every change and advance is

conditioned upon what precedes and surrounds it (Fig. 120). In the orchestra of developing parts a group of cells or an organ that is out of rhythm, like a blundering kettledrummer, may throw all the other performers into confusion and change a symphony into "discord."

The malformations and monsters which result from disharmony in growth and differentiation, are termed *terata*, and the somber science that concerns itself with such morphological misfits, is called *Teratology*. Terata may involve the entire individual, as in the instance of "Siamese twins" of various kinds, or they may concern only parts of individuals, or organs, as in such deformities as clubfoot or cleft palate. Finally, abnormalities may be simply groups of cells, like *tumors*, that have somehow lost step with the advancing host of correlating parts, and so fallen into disharmony. Such tumors, or uncoördinated members of the cellular state, are termed *benign* or *malign*, according to the degree and manner in which they encroach upon or injure surrounding tissues. Malign tumors, such as "cancers," constitute one of the most disastrous disharmonies to which mankind is subject, and much study and exhaustive research is being directed towards the understanding and control of these troublesome formative disturbances.

Under the heading of formative disturbances are also to be included modifications in growth, evidently associated with something wrong in the behavior of certain regulatory endocrine glands, as, for example, *dwarfism* and *giantism*.

B. Mechanical Interferences

Obstructional disturbances in the nutritional mechanism or the excretory apparatus, may also work ill to the organism. The circulatory system, for example, through which the individual needs of the cellular state are supplied, may suffer from local obstructions, blood deficiency, or interference with its nerve supply. When, for any considerable time a part of the body is deprived of the life-giving stream of food that is carried in the blood, by hemorrhage, or by such local obstructions as may result from congestion, pressure, wounds, or blood clots, there results a nutritive disturbance. If the siege is not raised eventually, starvation and death of the isolated tissues are the outcome. When such dead parts are exposed to ubiquitous putri-

factive organisms, *gangrene* may follow with serious consequences to the neighboring living tissues, while if there is protection from such foreign invasion, and the dead tissues are not too extensive, they finally become absorbed or are sloughed off, and normal conditions are restored. Interruptions in the stimulative service of the nerve supply, from paralysis, shock, or any other interference, are also the immediate cause of a myriad of nutritional woes.

C. Responsive Activities

By responsive activities are meant such functional disturbances as follow in the wake of internal maladjustments of one kind and another that interfere with physical performance. The response to overwork, for example, may cause an increase in the size and number of the component cells in an organ and result in *hypertrophy*, or excessive growth. If this response is called forth to meet a normal physiological emergency, as in the hypertrophy of the mammary glands during lactation, or of the uterus in pregnancy, then it is normal and lies outside of the field of pathology, but if it works ill to its possessor, like the modified valves and strained walls of the so-called "athlete's heart," then it becomes pathological.

Atrophy, either degeneration or arrest of growth, is an instance of nutritive disturbance that causes irregularity in the responsive activities. It usually follows a cessation of function, as when the optic nerve atrophies after the loss of an eye, or when a paralyzed leg or arm wastes away.

D. Hereditary Handicaps

Deviations from the normal that lead to disease may be of two kinds. First, they may be *acquired*, in a great variety of ways during the lifetime of the individual; or second, they may be *germinal*, that is, inherited from the ancestral streams of germplasm. Blindness, for example, may be acquired by accident any time before or after birth; or it may be germinal, as in the case of certain types of "congenital" cataract that "run in the family" and are inborn.

In the miscellaneous collection of germinal heirlooms that constitutes our heritage, there are bound to be some things that we wish we did not have. Every person in this imperfect world has at least one such "skeleton in the closet." Frequently the skeleton cannot be suppressed and concealed in a closet, but

must be painfully carried about in plain sight, like the burden on the back of Bunyan's immortal pilgrim.

Diseases as such, particularly bacterial diseases, do not cross over the tenuous bridge of germ cells which connects one generation biologically with another. *Constitutions and tendencies*, however, that insure the eventual sequence of disease, are a part of the hereditary equipment of everyone.

2. External Disturbances

Many of the causes of disturbance, that put the "pathos" into pathology, have their origin outside the individual in the form of various environmental factors, of which those described as thermal, chemical, barometric, mechanical, and biological, are representative.

A. Thermal Factors

Extreme variations from the normal limits of temperature to which any organism has become adapted, may result in *thermal* disturbances that work ill. Here belong the disastrous sequelæ of scalds, burns, and sunstrokes at one extreme, and frostbite or freezing at the other. The harm done in these disturbances may take the form of nervous shock, hemorrhage, or necrosis of the part involved, with subsequent invasion and infection by destructive bacteria.

B. Chemical Factors

Injurious chemical contacts, as in the case of ptomaines and various poisons introduced into the digestive tube, cause a variety of troubles. Painters and lead workers frequently suffer from lead poisoning, while phosphorus and other deleterious chemical substances carry particularly unfortunate consequences to the people who are continually exposed to them.

C. Barometric Factors

Deep-sea divers, mountain climbers, and aviators, who depart from the barometric environment to which they are normally attuned, harvest a crop of pathological protests as a result, and men in deep mines, or those engaged in tunnel construction who are forced to work for hours under abnormal atmospheric pressure, may acquire "caisson disease," which manifests itself in paralysis of the legs, profuse bleeding from the nose, ears and mouth, and in apoplexy.

D. Mechanical Factors

Outside mechanical agencies may bring about sudden injuries, or wounds, of varying degrees of seriousness from mere scratches to extensive disasters that include the destruction of so much of the body as to imperil life itself. The power to repair wounds of any kind varies greatly in young and old. In tissues that are comparatively undifferentiated it is greater than in those that have attained a considerable differentiation. The response of the body in repairing wounds, involving behavior of the cellular units concerned, is of particular interest to the pathologist.

Mechanical factors, instead of causing sudden wounds in the organism, may take the form of irritants that work more slowly and insidiously. Cancer of the lip, for instance, is said to be more frequent in the case of pipe smokers, who have subjected themselves for a considerable time to the local mechanical irritation of a pipestem, than among non-smokers.

Many occupations that involve the inhaling of irritating dust particles, like handling coal, threshing grain, cutting stone, and polishing steel, have characteristic disease manifestations as a consequence of mechanical irritants acting upon the respiratory machinery.

E. Biological Factors

There are three general kinds of parasites that may attack other organisms and upset their normal course of living. They are (a) pathogenic bacteria; (b) pathogenic protozoa; and (c) a heterogeneous group of larger parasites, including certain worms, insects and other harassing forms, that prey upon their betters.

The pathogenic bacteria are microscopic plants that cause such diseases as tuberculosis, cholera, diphtheria, tetanus, anthrax, and typhoid. The harm they do is usually the result of toxins, or poisons, which they set free in the tissues of their hosts during the course of their own metabolic processes, or when they die. They may, however, by sheer numbers resulting from their prodigious powers of multiplication, either plug up the capillaries in which they swarm, so that the circulation is impeded or prevented, as in anthrax, or they may induce the formation of a bulky mass that acts like a strangling gag upon their victim, as in diphtheria, or "membranous croup," as it was formerly called.

Beginning with Pasteur and Lister within the memory of people now living, the science of *Bacteriology*, which has to do with these minute foes of mankind, has so increased in importance and achievement that it has become indispensable in all modern medicine and surgery. There is no doubt that the future will see still greater triumphs and conquests in this fertile field of human endeavor.

The science of *Protozoölogy*, with its wide application to the control of diseases induced by pathogenic one-celled animals, has lagged somewhat behind the twin science of bacteriology, partly because the technique involved in obtaining pure cultures of organisms for accurate experimentation is more difficult. Nevertheless, much has been learned already, and greater discoveries and successes in this field surely await the investigator just around the corner. Many diseases are caused by protozoan parasites which infest the blood of their hosts, for example, malaria and the "sleeping sickness" of Africa, while the troubles following in the train of amebic dysentery are an instance of the consequences caused by protozoan highwaymen that infest the digestive canal.

Parasitology in general, out of which the flourishing young sciences of bacteriology and pathogenic protozoölogy have sprung, is now usually concerned with the larger parasites, like tapeworms, flukes, hookworms, and other worms, that take up their domicile in the bodies of their hosts, or such external visitors as ticks, lice, and fleas which Mark Twain said keep a dog "from thinking about being a dog."

IV. SOURCES OF PATHOLOGICAL KNOWLEDGE

A knowledge of the facts of pathology, which is contributing daily to the alleviation of abnormal conditions, is gained principally through clinics, autopsies, physiological and micropathological research, comparative pathology, and animal experimentation. *Clinics* include bedside experiences gained by actual observation of the abnormal conditions exhibited by the patient. *Autopsies* are post-mortem examinations of biological clocks that have stopped, in order to find out what has gone wrong with the machinery. *Micropathological research* is directed toward an intimate understanding of the behavior and appearance of cellular units when under abnormal conditions. It includes not only *Pathological Histology*, but also bacteriology and *Pathological*

Protozoölogy. Comparative Pathology recognizes the fact that even with human pathology as the objective, much is gained by an indirect method of approach through other members of the animal kingdom. Man is too complex a mechanism to be understood at once without some preliminary acquaintance with the simpler mechanisms of animal life. Moreover, pathology is much more than the science of human ills. It is a field of study in itself, fertile enough to promise rewards to the student of pure science whose eyes are not necessarily fixed on immediate utility. *Animal experimentation* has made possible not only a knowledge of the facts and principles of pathology, but has also cleared the way for the diagnosis and control of the pathological disturbances that beset mankind. Without recourse to animal experimentation the triumphs of modern medicine could never have come about.

It is unfortunate that the word "vivisection" in this connection has become such a bogey, for it has caused many people to remain uninformed or misinformed about a very important subject. The truth of the matter is well stated by Dr. W. W. Keen in a pamphlet entitled *What Vivisection has Done for Humanity* (1910), the concluding paragraphs of which are here quoted. "The alleged atrocities so vividly described in antivivisection literature are fine instances of 'yellow journalism,' and the quotations from medical men are often misleading. Thus, Sir Frederick Treves, the eminent English surgeon, is quoted as an opponent of vivisection in general. In spite of a denial published seven years ago the quotation still does frequent duty. I know personally and intimately Horsley, Farrier, Carrel, Crile, Cushing, and others, and I do not know men who are kinder or more lovable. That they would be guilty of deliberate cruelty I would no more believe than that my own brother would have been.

"Moreover, I have seen their experiments and can vouch personally for the fact that they give to these animals exactly the same care that I do to a human being. Were it otherwise their experiments would fail and utterly discredit them. Whenever an operation would be painful, an anæsthetic is always given. This is dictated not only by humanity, but by two other valid considerations; first, long and delicate operations cannot be done properly on a struggling, fighting animal any more than they could be done on a struggling, fighting human being, and so again their experiments would be failures; and second, should anyone try an ex-

periment without giving ether he would soon discover that dogs have teeth and cats have claws. Moreover, it will surprise many of my readers to learn that of the total number of experiments done in one year in England, 97% were hypodermic injections and only 3% could be called painful!

"'If anyone will read the report of the recent British Royal Commission on Vivisection he would find,' says Lord Cromer, 'that there was not a single case of extreme or unnecessary cruelty brought forward by the Antivivisection Society which did not hopelessly break down under cross-examination.'

"In view of what I have written above—and many times as much could be added—is it any wonder that I believe it to be a common sense, a scientific, a moral and a Christian duty to promote experimental research? To hinder it, and still more to stop it, would be a crime against the human race itself, and also against animals, which have benefited almost as much as man from these experiments.

"What do our antivivisection friends propose as a substitute? Nothing except clinical, that is, bedside—and post-mortem observations. These have been in use for two thousand years and have not given us results to be compared for a moment with the results gained by experimental research in the last fifty, or even the last twenty-five years.

"Finally, compare what the friends and foes of research have done within my own professional lifetime. The friends of research have given us antiseptic surgery and its wonderful results in every region and organ of the body; have abolished lockjaw, bloodpoisoning, erysipelas, hydrophobia, yellow fever; have taught us how to make maternity almost absolutely safe; how to reduce the mortality of diphtheria and cerebro-spinal meningitis to one-fourth and one-third of their former death rate, and have saved thousands of the lower animals from their own special diseases.

"What have the foes of research done for humanity? Held meetings, called the friends of research many bad names and spread many false and misleading statements. Not one disease has been abolished, not one has had its mortality lessened, not a single human life has been saved by anything they have done. On the contrary, had they had their way, puerperal fever and the other hideous diseases named above, and many others, would still be

stalking through the world, slaying young and old, right and left—and the antivivisectionists would rightly be charged with this cruel result."

V. THE CONTROL OF DISEASE

In the earlier days of human ignorance, disease was regarded as due to the presence of evil spirits, and cures were supposed to be effected when these malign visitors were properly exorcised by some conjurer or medicine man.

Although the conjurer in various guises still trades upon superstition and ignorance, the modern controller of disease has come to recognize that all methods of healing, almost without exception, resolve themselves simply into extensions of the natural phenomena of growth and repair that are inherent in the patient. For example, it has been found that by injecting dead cultures of the causal agents into subjects infected with a pathogenic organism, there is produced in the body fluids a substance (*opsinin*) which apparently in favorable conditions unites with the living causal bacteria, and so sensitizes them that they are readily taken up and destroyed by the phagocytic cells of the tissues. The afflicted body, therefore, *cures itself* whenever a cure is effected, and frequently nearly all that the modern "medicine man" can do is to intelligently direct the efforts of the body in its task of restoring normal conditions.

Three general directions in modern attempts to control disease may be pointed out, namely, by curative, preventive, and creative medicine.

Curative medicine, finding itself in a world of disease and disaster, sets out to heal the sick and to bind up the wounds of the injured. It has assumed a colossal task, and, like the good Samaritan that it is, has gone about the business with noble devotion and increasing success.

Preventive medicine, on the other hand, seeks to forestall trouble. For example, by vaccination diseases like smallpox are prevented, and by means of antitoxins the poison of invading germs, like that of diphtheria, is counterbalanced and rendered innocuous. Thus, protective immunity against disease is accomplished through the use of vaccines, antitoxins, opsonins, endocrine extracts, and other resources of the bacteriologist and the physiological chemist.

Creative medicine, which at present is hardly more than a dream, takes a long look ahead and attempts to prevent the abnormal with all its disastrous chain of consequences, by seeing to it that, as far as possible, only the normal are born into the world. This is the hopeful field of *Eugenics*, which seeks to lessen and prevent disease by providing an hereditary equipment, able to maintain itself triumphantly harmonious in the face of besetting discords.

All of these lines of possible betterment must advance through the frontier land of pathology, hence its importance in the survey of things biological.

PART TWO

THE MECHANISM OF METABOLISM AND REPRODUCTION

CHAPTER X

A JACK OF ALL TRADES (THE INTEGUMENT)

I. IN GENERAL

In making a study of the structures of the body it is fitting to begin with the integument because, like the wrappings around a parcel, it is the first part to be encountered in an examination of any animal. It is, however, much more than a mere wrapping enclosing organs within, for it is in itself an "organ," just as definitely as is the liver, heart, or brain, and as a matter of fact, it is a very versatile organ serving a great variety of purposes.

The integument may be described as a *compound* organ. *Morphologically* it is compound because it is structurally double, being made up of *epidermis* and *corium*. *Embryologically* its compound character is indicated by its derivation from two separate germ layers, namely the *ectoderm* from which the epidermis arises, and the *somatic mesoderm*, from which comes the corium (Fig. 112). *Physiologically* the integument is a versatile organ, since it performs a wide range of functions and is consequently comparable to a "jack of all trades."

The vertebrate integument consists of the skin and its derivatives. The outside of the body, including even the exposed surfaces of the eyeballs, is entirely clothed with integument. At the nose, mouth, anus, and genital openings it passes over into a related tissue, the *mucous membrane*, which lines passage-ways. Tissues composing the integument are more or less stratified into layers. The adaptations exhibited by the outside layers which face the environing world, are very different from those of the deeper layers which are necessarily more influenced by underlying organs than by outside surroundings.

II. USES OF THE INTEGUMENT

Among the various uses for which the structure of the integument is adapted in different animals, are the following: (1) protection; (2) reserve food storage; (3) heat regulation; (4) sensation; (5) excretion; (6) secretion; (7) respiration; (8) locomotion; (9) sexual selection; and (10) reproduction.

1. Protection

Four aspects of the protective function of the integument may be mentioned. First, it shields the animal body against *mechanical injuries* which may result from pressure, friction or blows of various sorts. Like any other wrapper, the primary function of which is to protect the enclosed parts, the vertebrate integument is admirably adapted for this purpose, since it is typically closely woven in texture, and resistant, while at the same time it is pliable and elastic so that it tends to "give" under mechanical stress rather than to rupture or break away.

In addition to the enveloping skin itself, most animals are equipped with protective integumentary modifications of some kind, such as scales, bony plates, feathers, hair, or cushions of fat which aid in minimizing the effects of blows and injurious contacts of various kinds. Invertebrates, such as crustaceans and molluscs, are conspicuously fortified by *exoskeletons* against an unfriendly world, while turtles, armadillos, alligators and porcupines are noteworthy instances among vertebrates of animals that go forth, like armored knights of old, well clad to resist the blows of their adversaries.

Second, the integument protects the body *against foreign substances*. Whenever skin infection from any foreign source occurs, it is usually through some break, however slight, in the protective integument. So long as the skin remains whole it is practically germ proof.[4]

Cleaning the skin of whatever undesirable things may stick to it, usually accomplished by civilized man with soap and water, is managed by the unsaponified relatives of man in a variety of ways. The production of mucus over the skin of certain fishes and amphibians, for example, makes a constantly removable jacket which, in sloughing off, carries foreign accretions with it. In various ways also the outermost dead layers of the skin, with

such epidermal structures as hair and feathers, are periodically cast off. When a snake "sheds its skin," although only the outermost part of the epidermis is involved, it emerges bodily clean from the gauzy corneal envelope which it leaves behind like a soiled garment.

Third, the skin protects the body from *excessive loss of moisture.* This is very important since in living tissues water plays a major rôle. The protoplasm in every cell must retain a certain degree of fluidity or it dries up and dies. Moreover, water is the basis for all internal transport of material, as well as the great chemical solvent of the substances to be transported. These precious underground waters of the body are conserved very largely by means of the waterproof blanket of the integument. Its impervious character serves not only to retain moisture within but to keep out an unregulated amount of water in the case of submerged animals such as fishes, whose more delicate underlying tissues would become water-soaked without such protection.

Fourth, the skin or integument acts as an organ of protection in all those animals exhibiting "*protective coloration,*" whereby some degree of invisibility, and consequent escape from enemies, is secured by close resemblance to the surroundings. So-called "*warning colors,*" like the conspicuous black and white markings of a skunk, which serve as "hands off" signals to their possessors, are similarly integumentary modifications, protective in function.

2. Reserve Food Storage

In the deeper subcutaneous layers of the skin, reserve food in the form of fat is stored, to be drawn upon, like a savings-bank account, in times of need. The manner of its irregular distribution in cushions and pads constitutes the basis of those contours in "the outward form and feature" that have pleased the eye of artists from time immemorial, and suggests an anatomical reason for the familiar phrase, "beauty is only skin deep."

In man this stored subdermal fat may constitute as much as 20% of the entire weight of the body. In whales and seals it forms an extensive blanket of considerable thickness, called *blubber,* that not only serves as food storage, but also acts as a non-conducting retainer of body heat.

3. Heat Regulation

Heat is being constantly generated by the oxidation of tissues within the animal body. Coming faster from soft parts like muscles than from hard parts like skeletal organs, it is distributed and equalized by the flowing blood which permeates nearly every part of the body, so that in "warm-blooded" animals, a practically constant temperature is maintained. From such an animal, heat is lost in three ways, with the expired breath, with the excreta, and from the skin.

Every warm breath carries away a certain amount of body heat, for cold air that is drawn into the lungs is warmed at the expense of the body before it is expired. The excreta, both urine and feces, are kept at body temperature until expulsion, when therewith a loss of heat occurs. Perhaps nine-tenths of the heat loss, of a warm-blooded animal like a mammal, however, is through the skin. Heat regulation is consequently very largely an integumental function.

The skin effects the regulation of heat loss in two ways, one physiological, the other physical. *Physiological regulation* is brought about by the expansion or relaxation and contraction of the skin and of the walls of the capillaries contained therein. In cold air the skin tends to contract, sometimes to the point of forming "goose flesh," and consequently the capillaries carrying the warm blood are buried somewhat from the surface and are contracted to a smaller size. The amount and degree to which the circulating blood is exposed is thus diminished and there is a lessened loss of heat. In warm air the skin relaxes, the capillaries are more exposed and their walls more expanded so that there results a greater opportunity for the loss of heat.

Physical regulation is accomplished by the evaporation of sweat which is constantly being excreted from the mammalian skin, even though it does not always appear as visible drops. Heat is always required in the physical process of changing a liquid into a gas. In the evaporation of sweat the necessary heat is abstracted from the skin and thus lost from the body. Heat loss from the body is further controlled by the fact that parts of the integument, like the blubber of the whale, serve as a non-conducting blanket to hold in the heat.

In birds the dissipation of heat is regulated through a cover-

ing of adjustable feathers by means of which a blanket of warmed air may be retained next the skin. The same thing is accomplished in the case of civilized man by means of clothing, which in reality is nothing more than an extra layer of non-conducting, artificial integument added to that which nature has provided.

4. Sensation

The most universal of all the senses, the great confirmatory sense of *touch*, has its receptors located in the skin. The allied sensations of pressure and temperature are also referable to integumental nerve endings, while even the chemical sense organs of taste and smell, which occupy the neighboring mucous membranes of the nose and mouth cavity in higher forms, are still found on the outside of the body in the skin of the lower aquatic vertebrates.

5. Excretion

In mammals the sweat glands supplement the kidneys in removing waste products from the blood. Each sweat gland in the skin, with its accompanying capillary, is a complete kidney apparatus in miniature. Whenever the activity of the sweat glands is accelerated by exercise, heat, or diuretic drugs, there is less work for the kidneys to do.

6. Secretion

The mammary glands more than any others mark the skin as an organ of secretion. There are also present in the mammalian skin, associated with hairs, a great number of sebaceous, or oil glands, that are secretory in function.

Other instances of the integument as an organ of secretion, particularly among the invertebrates, could be given, such as the "crust," or exoskeleton, of the Crustacea, which is a secretion of the hypodermis, or skin.

7. Respiration

Among the amphibians the skin accomplishes to a remarkable degree the exchange of gases which constitutes respiration. The *cutaneous arteries* supplying the skin of a frog, for example, are larger than the *pulmonary arteries* that go to the lungs.

Gills may be regarded morphologically as extensions of the skin, and the *tracheæ*, or breathing tubes of insects, also come under the head of integumental structures.

8. Locomotion

In the great and diversified group of Arthropoda, which includes much over half of all known kinds of animals, locomotion is accomplished by means of lever-like appendages, the actuating muscles of which are attached to the integumentary exoskeleton. The wings of insects are entirely integumentary.

Among vertebrates the wing and tail feathers of birds, that are essential to flight, are also integumentary in origin. The skin takes conspicuous part too in the wings of bats, and the flying mechanism of all parachuting animals, such as flying squirrels, flying lemurs and the "flying dragon" of India (*Draco*), as well as in the wings of the extinct *Pterodactyls*, which had skin stretched between the little finger and the sides of the body. Animals with webbed feet like ducks and frogs depend upon skin between their toes to make the paddles that propel them through the water.

9. Sexual Selection

Among higher animals, particularly birds, there is frequently a marked difference in the appearance of the sexes, due usually to integumentary modifications in the color or form of the skin. Darwin's "Theory of Sexual Selection," was brought forward as an explanation of these differences. Briefly, according to this theory, a rivalry exists between males for the possession of their mates. Those males that make the best showing, that is, those performing the most convincing antics or presenting the most attractive integument before the critical females, become the successful suitors and leave descendants which carry on their winning features. Although the theory of sexual selection has been greatly criticized, its validity or non-validity does not affect the fact that many conspicuous distinctions between the sexes, whatever their use may be, are integumental in character. Odors also, of various kinds, arising from glands located in the skin, serve as excitants in the sexual behavior of different animals.

10. Reproduction

Among insects the copulatory organs, which are employed in reproduction, are almost entirely integumentary in origin. While this is not true of vertebrates, integumentary contact and the skin odors already mentioned both play an important sensory rôle in the mating behavior of various higher animals.

III. THE HUMAN SKIN

1. Macroscopic

The human skin as a whole conforms to the underlying parts of the body as a continuous organ. It is interrupted only at the ends of the alimentary canal, where it extends inward as mucous membrane, and at the openings of the reproductive and excretory

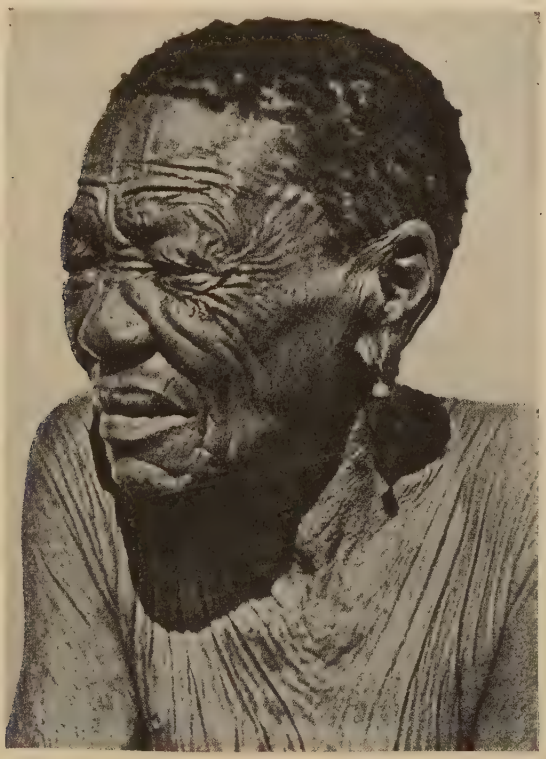


FIG. 121.—A Hottentot, showing the wrinkled skin of old age, and kinky hair. (After Martin.)

organs. Its smooth expanse is diversified by a few noteworthy elevations and depressions, for example, as it is stretched over the cartilaginous framework of the external ear, and as it descends into the ear passage itself. The innumerable tiny pits which appear whenever there are emerging hairs or openings of sweat glands, are microscopic depressions in the skin that do not entirely pene-

trate it or in any way interrupt its continuity. The eyelids are composed principally of conspicuous folds of skin, while a great number of wrinkles and creases, particularly around the joints, aid in accommodating the elastic integument to changing contours. In old age the skin frequently exhibits wrinkles because it does not shrink as rapidly as the underlying muscles do in the process of diminishing repair attendant upon advancing years (Fig. 121).

The skin is *thinnest* where it passes over the exposed part of the eyeball. It is so thin and translucent in the eyelids that it is even possible to perceive light through three layers of skin at once, for, when one turns closed eyes towards a brilliant light, the difference between light and darkness may easily be distinguished through the conjunctiva that passes over the cornea and the double fold that constitutes the eyelid (Fig. 122).

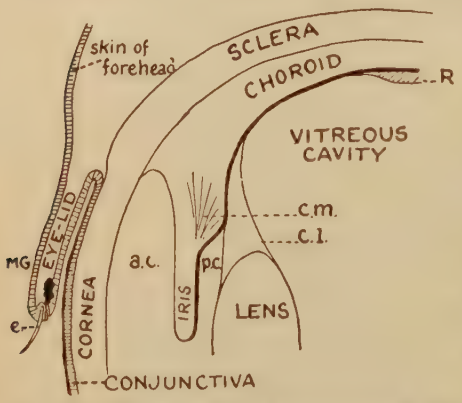


FIG. 122.—Diagram of the conjunctiva of the eye, showing its continuity with the skin *via* the double fold of the eyelid. *c.m*, ciliary muscle; *c.l*, ciliary ligament; *a.c*, anterior chamber; *p.c*, posterior chamber; *M.G*, Meibomian gland; *e*, eyelash; *R*, retina.

The *thickest* region of the skin is on the soles of the feet. The natural thickness may be increased by use, as is repeatedly demonstrated by corns, callouses and other local thickenings, wherever there is continued excessive friction or contact, as in the soles of the habitually unshod. According to Lamarck, the thickened skin on the sole of a baby's foot is inherited from ancestors who acquired it while walking up and down the earth. This is by no means, however, the only possible, or the most plausible explanation. Mud puppies (*Necturus*) likewise have the thickest skin on the soles. Since these primitive salamanders live always in water, they do not "use" the soles of their feet, nor is it likely that any of their ancestors have done so. Obviously there must be another reason for the differentiation in skin thickness on the soles of the feet.

According to Rauber the *area* of a typical adult human skin

is about 1.6 square meters, or approximately five feet square. This fact is instructive when it is remembered that certain functions of the skin, as an organ of excretion or respiration, for example, depend upon its expanse.

The *weight* of the human skin, with the subcutaneous fat removed, as determined in autopsies, is stated by Bischoff to be 3,175 grams for a female twenty-two years old, and 4,850 grams for a male thirty-three years old, or approximately from 7 to 10.7 lbs.

The *color* of the skin depends upon two factors, namely, its translucency, which permits the underlying capillaries to show through, as in blushing, and the presence of pigments. These pigments, of which there are yellow, black, and red kinds, are all present in varying proportions in the different races of mankind except albinos, and even in a single individual are unequal in their distribution, being deeper on exposed parts of the skin, and around the axillæ, nipples, and genitalia. The color of the skin varies also with age, from pink babyhood to yellow old age.

2. Microscopic

Although the two fundamental layers of the skin, the *epidermis* and *corium* or *derma*, lie against each other in intimate contact, yet they have quite different origins, modifications, and uses.

A. Epidermis

From the beginning the epidermis, which is derived from the embryonic ectoderm, is the outermost investment of the body. Its most important component is the deepest layer of cells next the corium, because these cells, with remarkable reproductive energy and persistence, produce not only the entire epidermis, but also such accompanying accessory modifications as hair and nails. This germinative layer has been called the *Malpighian layer* (Fig. 123), in honor of Marcello Malpighi (1628–1694), who first pointed out its significance, thereby erecting to his name a monument far more enduring than an isolated mausoleum or marble shaft.

The progeny arising from the successive divisions of the parent Malpighian cells, are gradually modified while they are being crowded toward the exposed surface of the skin. The cell walls become somewhat thicker, the nuclei break down, accompanied by a series of chemical changes in the substance of the cell itself, the body of the cell flattens, and eventually only a dead trans-

formed remnant remains, like the collapsed skin of a grape after the pulp has been squeezed out. The squamous husks of the dead cells thus formed are constantly breaking free from the underlying cells and being shed, while a continual renewal from below is maintained from the base line of the Malpighian layer. Sometimes when the skin "peels" after sunburn, the dead epidermal cells hang together in sheets and strips, and are shed somewhat in the manner that a snake "sheds its skin."

This dead outer layer is called the *corneum*, the chief constituent of which is *keratin*. The region between it and the living Mal-

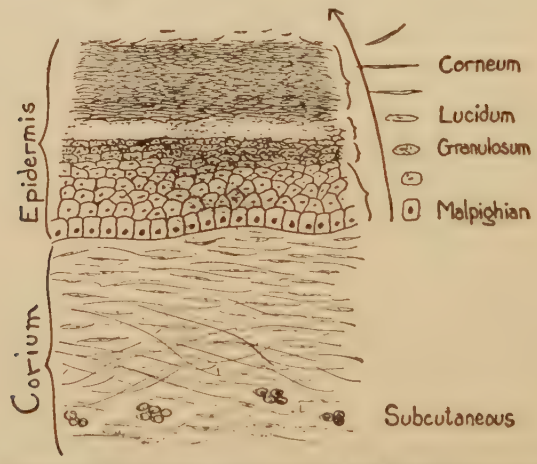


FIG. 123.—Diagram of the skin, showing how the Malpighian layer gives rise to the superimposed layers of the epidermis.

pighian cells below is characterized in certain areas of the body by the insertion of two transitional "layers," termed the *stratum granulosum* and the *stratum lucidum*. The stratum granulosum is best seen on the soles of the feet and the palms of the hands, where cross sections of the skin show it to be two or three cells in thickness next the Malpighian cells. It is called "granulosum" because, upon the breakdown of the nuclei, *kerato-hyalin* (Waldeyer) granules are formed, which give it an appearance of greater density.

The apparently homogeneous stratum lucidum, which lies just outside the stratum granulosum and is derived from it, owes its semi-transparency and comparative resistance to all ordinary stains to the fact that the kerato-hyalin, coming from the stratum

granulosum, changes into a different chemical compound called *eleidin* (Ranvier). The stratum lucidum is usually wanting except where the skin is particularly thick, but it reaches a conspicuous development in the nails which it principally composes.

The stratum corneum, together with the intermediate strata, lucidum and granulosum, when present, furnishes a buffer between the delicate living cells of the Malpighian layer and the outside world.

Only in exceptional cases do blood vessels penetrate the epidermis, so that whatever food it receives must be passed to it osmotically from neighboring dermal capillaries. This helps to explain why a Malpighian cell becomes more and more dead the farther away it lies from the corium.

Sensory nerve endings, except those of the most undifferentiated character, do not ordinarily extend into the spaces between epidermal cells, so that stimuli which affect the body must reach the deeper-lying nerve endings of the corium *through* the protective barrier of the epidermis.

Skin pigment is usually located in the Malpighian layer of the epidermis.

B. Corium

The *corium*, or the distinctive part of the vertebrate skin, is a connective tissue network consisting of cells and fibers produced by cells felted together. It underlies the superficial epidermis and is many times thicker. When leather is tanned the corium is the part of the skin that is utilized.

Many structures are embedded in the corium, for example, capillaries, lymph vessels, nerve endings, dermal sense organs, migrating pigment cells, deposits of fat and glycogen, smooth muscle fibers, sweat glands, sebaceous glands, and hairs.

Beneath the corium and transitional with its deeper layers is the *subcutaneous layer*. It is characterized particularly by the inclusion of masses of soft, fat cells and by the looser weave of the felted reticulum, which allows greater freedom of motion to the underlying muscles. Some of the fibers of the subcutaneous region interlace with the fibers composing the connective-tissue sheaths surrounding the muscles, thus fastening the skin down, as it were, more firmly. This is demonstrated better in the palm than over the back of the hand where the skin is looser.

In regions of the body, such as the finger tips, that are much in contact with things, the outer part of the corium next the epidermis is thrown up into rows of tiny projections, or *papillæ*, that form ridges (Fig. 124). It is customary, consequently, to speak of the *papillary layer* of the corium. The roughened papillary layer perhaps helps to hold the corium and the epidermis together at points on the skin where friction or pressure is frequently ap-

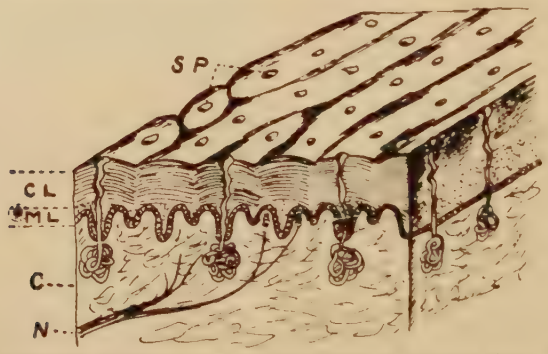


FIG. 124.—Diagram showing some of the details of friction skin. The ridges on the surface are penetrated by the pores of the sweat glands, which lie coiled up in the corium below. Two sensory papillæ are shown. *SP*, sweat pores; *CL*, corneal layer of epidermis; *ML*, Malpighian layer of epidermis; *C*, corium; *N*, nerve of touch. (After Wilder and Wentworth.)

plied, for the epidermis dovetails intimately into the minute hills and valleys formed by the papillæ.

There are two sorts of papillæ in this outside layer, namely, *nutritive* and *sensory*, the former containing a capillary knot, the latter occupied by a sensory nerve ending. It is possible to distinguish these two kinds of papillæ in the finger tips experimentally by patient manipulation with a very fine needle. When a nutritive papilla is punctured there is no particular pain although a tiny drop of blood may appear. When a sensory papilla is pricked no blood flows but pain is felt.

Whenever papillæ are present it is possible to distinguish three "layers" in the corium, which shade imperceptibly into each other, namely, *papillary*, *reticular*, and *subcutaneous*.

3. Embryonic

As already indicated, the human skin as well as the vertebrate skin in general has a double embryonic origin. The epidermis, which is the primary component, arises from that part

of the ectoderm remaining after the medullary tube, that forms the central nervous system, has migrated in from the outside by invagination. It consists at first of a single layer of ectodermal cells which soon gives rise to the *epitrichium* (Fig. 125), a delicate outer layer of somewhat enlarged cells that take certain stains distinctively and thus show a specific character. Corneal cells, derived from the Malpighian layer, soon appear under the epitrichium until, at the age of about three months in the human embryo, the epidermis of the fetus has become three or four layers deep. About the fifth month, when embryonic hairs begin to emerge from the skin, the gauzy epitrichium is shed from the entire body, except the palms and soles, and is never renewed. The name "epitrichium" (*epi*, upon; *trichium*, hair) signifies that it temporarily rests upon the tips of the budding hairs. A more inclusive term for this evanescent embryonic mantle is *periderm* (*peri*, around; *derm*, skin), since it is also present as a part of the embryonic skin of reptiles and birds where there are no hairs for it to rest upon.

FIG. 125.—Skin from the head of an embryo of 2½ months. The irregular dark outer layer is the epitrichium. *e*, epidermis; *c*, corium.

The corium comes from cells of the somatic mesoderm and the mesenchyme, and is secondarily wedded to the epidermis, which it eventually exceeds many times in thickness.

IV. COMPARATIVE ANATOMY OF THE INTEGUMENT

1. Invertebrate Integuments

The tiny bodies of the protozoa are without a true integument, although even in *Ameba* there is a clearer marginal area, the *ectoplasm*, which is different from the more granular inner part, or *endoplasm* of the cell.

In other invertebrates, that expose a cellular covering to the outside world, the integument is entirely *ectodermal* in origin, the mesodermal component being absent. No one has ever heard of leather being made from any backboneless animal, for leather is manufactured from the mesodermal (corium) part of vertebrate skin, and there is no such thing as invertebrate corium.

The simple invertebrate skin is called *hypodermis*, in distinction to the epidermis and corium of the compound vertebrate skin. The hypodermis may consist of but a single layer of cells of flat epithelium, as in sponges and many cœlenterates; of columnar epithelium, as in worms generally (Fig. 126); or

Fig. 126.—A section through the skin of an earthworm. *c*, *cuticle*, secreted by the hypodermal cells; *H*, hypodermis; *M*, muscles. (After Schneider.)

of ciliated epithelium, as in flatworms. Sensory and gland cells of various kinds may be interspersed between the other cells of the hypodermis, and so be in a position to come into relation with the environment. Frequently the hypodermis secretes a more resistant outer coat of chitinous, limy, or other substance, that is not in itself cellular but which comes to constitute an integumental exoskeleton. This is particularly the case with arthropods and molluscs. As the body increases in size within such an unyielding, integumentary armor, it becomes necessary

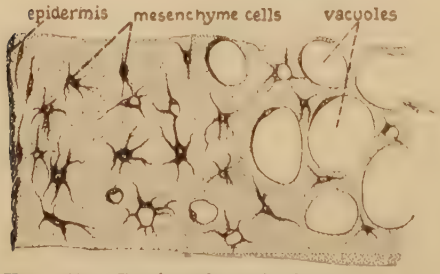


Fig. 127.—Section through the mantle of a tunicate, *Phallusia*. The wandering mesenchyme cells secrete the intercellular *tunicin*. (After O. Hertwig.)

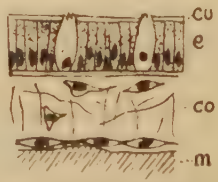


Fig. 128.—Section of skin of amphioxus. *cu*, cuticle; *co*, corium; *e*, epidermis; *m*, muscle. (After Haller.)

for the hypodermis to loosen periodically and to cast off the dead unaccommodating, secreted envelope, renewing it on a larger scale. Reminders of this process of *ecdysis*, or "moulting the skin," typical among arthropods, still persist even among vertebrates in the various ways in which dead corneal cells are sloughed off from the epidermis.

Molluscs, unlike arthropods, do not undergo ecdysis, but retain, with unfortunate parsimony, the exoskeletal shell secreted by the hypodermis, until they become so weighted down, by adding layer after layer, that locomotion is difficult and sensation largely superfluous. Eventually sedentary contentment and degeneration take the place of the natural evolutionary consequences of a more active and explorative existence.

2. Tunicates

Among ascidians or tunicates, which occupy a border-land position between vertebrates and invertebrates, the epidermis is much like the hypodermis of lower forms, because of its power to secrete non-cellular material (Fig. 127). The substance secreted is called *tunicin*, and it is not encountered elsewhere in the animal kingdom, although a chemically similar substance, *cellulose*, is a common constituent of plant tissues. Into the tunicin matrix thus secreted, along with blood vessels and nerves, wandering, irregular, mesenchyme cells penetrate, adding to the protective toughness of the mantle or tunic which gives these animals their general name of "tunicates."

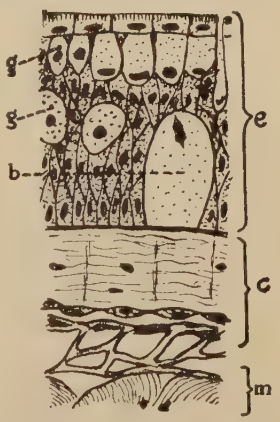


Fig. 129. — Diagrammatic section through the skin of a lamprey eel, *Petromyzon*. *b*, beaker gland cell; *c*, corium; *e*, epidermis; *g*, granular gland cell; *m*, underlying muscle. The outer layer of epidermal cells show striations; which are suggestive of the cilia of some invertebrate skins. (After Haller.)

3. Amphioxus

In amphioxus the compound integument, characteristic of the vertebrates, is reduced to its simplest expression. The epidermis consists of a single layer of columnar cells which, in the larval stage, are ciliated, as in certain worms, and later produce a thin non-cellular *cuticle* that is reminiscent, at least, of the exoskeletal structures secreted by the hypodermis of invertebrate forebears. Thus amphioxus, in assuming the dignity of a vertebrate, does not entirely burn its invertebrate bridges behind itself.

The corium in the skin of amphioxus is a thin layer of gelatinous connective tissue overlying the muscles (Fig. 128).

4. Cyclostomes

The slippery lampreys and hagfishes specialize in a highly glandular skin (Fig. 129). There are no scales present to restrict or modify the abundant and characteristic glands, which are of various kinds, principally mucous, and are distributed among the cells of the thick many-layered epidermis.

Fig. 130.—Suctorial mouth of *Petromyzon*, showing horny teeth and piston-like tongue. (From Gegenbaur, after Heckel and Kerr.)

Epidermal cells in the cyclostome skin, from the germinative Malpighian layer to the outside, do not exhibit the same sort of progressive modification toward a lifeless corneal condition that is typical of the mammalian skin, since even the outermost cells retain their youthful cytoplasm and are active enough to secrete a thin cuticle over their exposed surfaces, a lingering trace, perhaps, of long-vanished invertebrate days.

The horny teeth of cyclostomes (Fig. 130), form an exception to the apparent lack of epidermal cornification. They are periodically shed and renewed in the orthodox fashion of other corneal structures and are to be regarded as corneal modifications of the epidermis.

The corium, which is thinner than the epidermis in these aberrant fishes, is an interwoven meshwork of vertical and horizontal connective tissue fibers, practically undifferentiated.

5. Amphibians

The amphibian skin has much in common with that of cyclostomes, being highly glandular, scaleless, and with a relatively thin corium (Fig. 131). The epidermis, although consisting of several layers, is still thinner than that of the cyclostomes. The glands, however, are of a more complicated type, being composed of several cells each, instead of only one cell as in the cyclostomes. Although arising in the epidermis, the compound integumental glands of the amphibians do

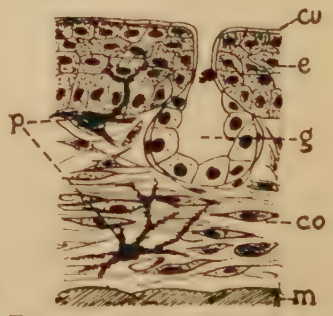


Fig. 131.—Section through the skin of a frog. *cu*, cuticle; *co*, corium; *e*, epidermis; *g*, compound mucous gland; *m*, muscle; *p*, pigment cells. (After Haller.)

not remain in an epidermal position, as the skin glands of cyclostomes do, but push deeper down into the corium. Being transitional animals, in and out of the water, their plentiful glands help to keep the skin moist and thin enough for respiratory service. The vascularization of the amphibian skin is particularly pronounced during the critical period of metamorphosis, when, in some cases, the unusual condition of penetration by capillaries of even the epidermis itself takes place.

Among the higher amphibians, which spend much of their life out of the water, the *corneum* is differentiated in the epidermis and a consequent ecdysis occurs, the dead outer layer shedding off in rags and tatters. A secreted invertebrate-like cuticle, such as amphioxus and the cyclostomes show, is present only transiently in larval amphibians, no longer appearing in the adult forms.

Pigment cells of the amphibian skin are mostly located in the corium, where they come under the control of the nervous system so that certain species, like the tree frogs, for example, are able to adapt themselves with considerable success to the color of the background in which they find themselves, thus escaping detection. It should also be noted that the skin glands of "warty" toads take on an irritating or even poisonous function, which discourages the advances of molesting enemies.

6. Scaly Forms

In many vertebrate species scales form a conspicuous modification of the integument. The character of the different kinds of scales will be considered in a later paragraph. In this connection attention will be directed simply to some of the typical integumental features of vertebrates with scaly skins.

A. Fishes

Most fishes possess scaly skins. Aside from scales, the integument of fishes is generally characterized by the closeness with which it fits the underlying parts. There is a tailored snugness about the skin of a fish that is not apparent in the baggy jacket of a frog, the loose integument of a bird, or the comfortable wrinkles of the mammalian skin.

The epidermis of fishes is highly glandular. A majority of the epidermal glands are superficial one-celled structures outside the

scales (Fig. 132), which serve to anoint the body with mucus. Although prophetic indications of a corneum are found in some instances among fishes, in general the epidermis, as in the cyclostomes, does not differentiate a definite external corneal layer, because a dead corneum is an adaptation to life on land and exposure to dry air.

The corium of fishes is a typical connective-tissue meshwork, more stratified in its deeper parts, and bearing the embedded scales to which it gives rise. Frequently the corium, as well as

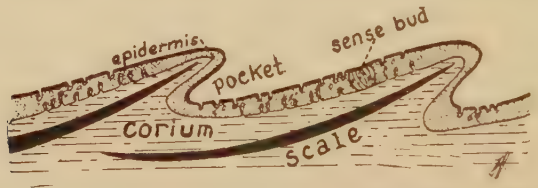


FIG. 132.—Long section through the skin of a teleost, *Barbus*. (After Maurer.)

the epidermis, displays pigment of different kinds which decorates the body with an endless variety of patterns and colors, particularly in brilliant, bizarre, tropical fishes.

B. STEGOCEPHALI AND APODA

In the evolution of the Amphibia it appears that multicellular glands have displaced scales as the most characteristic features of the skin. These two structures are, to a considerable degree, mutually exclusive. A truly glandular skin would be hampered by the presence of scales, and a scaly skin has no convenient place for glands. The tiny one-celled mucous glands over the surface of the scales of a fish are not to be compared in this connection with the dominant many-celled glands that characterize the amphibian skin.

Extinct amphibians of the Carboniferous Age (*Stegocephali*) were as scaly as any of their contemporary fishlike neighbors. They were large creatures, resembling salamanders in form though not in size (Fig. 25), and were conspicuously clothed with a cumbersome platelike armor quite in style, for they lived in the scaly times when defensive knighthood was in flower.

Among modern amphibians, however, only the degenerate, tropical cæcilians (*Apoda*) have any suggestive trace of scaliness.

The cylindrical bodies of these small wormlike animals are encircled with bands of tiny scales embedded in the skin, alternating with areas of typically glandular character (Fig. 133). Thus, in the skin of these lowly, inconspicuous bearers of the amphibian name, is written the final episode of the evolutionary story of the rout of the scales by the glands.

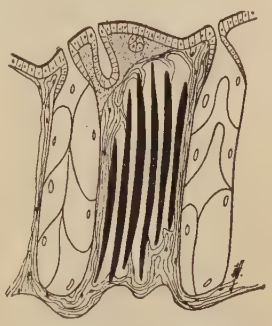


Fig. 133.—Section through the skin of an apodan amphibian, *Ichthyophis*. The scales, embedded in the corium, are in black, between two giant gland cells. Two smaller epidermal glands projecting into the corium, are represented near the surface. (After P. & F. Sarasin.)

C. Reptiles

The high-water mark in the completeness and elaboration of a scaly skin is reached by reptiles. One has only to examine with care the pattern, sculpture, and arrangement of the scales on a snake or a lizard to be impressed with their exquisite perfection.

The reptiles as a group are definitely committed to life on land, in spite of certain backsliding exceptions, and this fact has left its modifying impress upon the skin, which is no longer thin, moist, and respiratory, but thick and cornified against exposure to dry air. In the group of the reptiles the struggle for place between scales and glands has had quite a different issue than in the amphibians, for reptiles, with their inadequate legs, habitually rub much against the ground, and so have use for a corneal skin to safeguard them against frictional contact and dessication in dry air. Ecdysis is necessary for the removal of the dead outer layer of the epidermis, and integumental glands, which are superfluous in a highly cornified skin, are found only in exceptional cases as relics of the days before the ascendancy of scales.

Some of the extinct reptiles, for example, ichthyosaurs and pterodactyls, apparently had a scaleless skin, but most of the dinosaurs and their Mesozoic relatives were burdened with an enormously developed integumentary armor made up of large, dermal plates (Fig. 33, D), which were usually embossed in *bas relief*, and sometimes even bore along the back formidable spines projecting upward two or more feet.

In modern reptiles the corium plays a secondary rôle, while the epidermis reaches perhaps a greater elaboration than in any other group of vertebrates.

D. Other Scaly Vertebrates

Among birds and mammals scaliness is of exceptional occurrence. The scaly legs and feet of feathered birds (Fig. 134), reveal their reptilian ancestry, while there are a few scale specialists among mammals, as for example the armored armadillos of South America and the scaly anteaters of Africa. The skin of the fetal brown bear is scaly all over, with hairs interspersed (Fig. 135), and rats, opossums, and beavers have scaly tails that are conspicuous emblems of ancient allegiances which the comparative anatomist who runs may read.

Fig. 134.—Scaly foot of an osprey. (After Schäff.)

Fig. 135. — Embryo of brown bear, 4.5 cm. in length, showing a temporarily scaly skin. (After Haeckel.)

7. Birds

Anyone who has ever practiced taxidermy knows how loose, thin, and easily torn is the skin of a bird. Those parts not covered with feathers, like the shanks and the bare area around the base of the beak, exhibit a thickened corneal layer of the epidermis, but everywhere else not only the epidermis but also the corium is reduced to a delicate thinness.

The typical looseness of the bird's skin, so unlike the tightly fitting integument of the fishes, is an advantage in flight, for the muscles, unhampered by a binding integumentary sheath, are free to contract and change their shape easily. The looseness of the skin of penguins serves a special purpose adapted to icy antarctic conditions. During incubation the single egg is lifted off the cold ground to a secure position on top of the webbed feet of the parent bird and a generous apron of loose skin from the belly region is snugly wrapped around the egg to keep it warm (Fig. 136).

Exoskeletal structures of birds, such as feathers, beaks, scaly legs, claws, etc., are entirely epidermal, for dermal elements, like the scales of fishes or the bony plates of certain reptiles, are absent in this group.

Glands, already scarce in the skin of reptiles, are entirely wanting in the bird's skin, with the exception of the *uropygial* oil gland at the base of the tail. Even this gland is missing in the running birds (*Ratitates*), parrots, and many species of pigeons.

8. Mammals

The essential features of the mammalian integument have already been indicated in the section on human skin. It may be emphasized here, however, that among mammals the corium reaches its greatest development, becoming many times thicker than the epidermis. The conspicuous modifications of the mammalian epidermis are hairs and glands, and these structures, with others, will be considered in the next section.

FIG. 136. — A king penguin tucking the solitary egg into the "pouch" after relieving its mate. "These birds build no nests, but carry their single egg on top of their feet, covering it with a flap of skin. If the bird is robbed of its egg, it will attempt to mother a stone." (After Murphy, in *National Geographic Magazine* of April, 1922.)

V. DERIVATIVES OF THE INTEGUMENT

1. Glands

A. In General

Glands are cellular structures that produce a secretion or excretion. They may consist of single cells which have gone farther than their ectodermal neighbors in glandular specialization, or they may be composed of groups of similar cells that join in the common enterprise of producing some kind of a substance which is of use to the organism as a whole.

Some glands, such as the sebaceous hair glands, are called *necrobiotic*, because they use up their cellular substance in the production of their secretions and, after having thus exhausted themselves, need to be replaced by successors. Another type,

like sweat glands, for example, are *vitally secretory*, that is, they continue to elaborate secretions without fatal results to their component units.

Among vertebrates all the various kinds of integumentary glands take their origin in the Malpighian layer of the epidermis. In the lower forms they have at first only a surface exposure, as in the mucous glands in the hypodermis of an earthworm, but as glandular needs increase and the amount of available outside surface becomes inadequate, they push down into the underlying

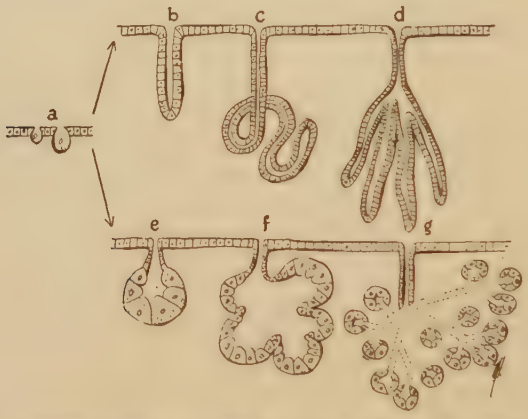


Fig. 137.—Diagrams of various types of glands, shown as invaginations from a layer of indifferent epithelium. *a*, primitive unicellular glands; *b*, simple tubular gland; *c*, coiled tubular gland; *d*, branched tubular gland; *e*, simple alveolar gland; *f*, compound alveolar gland, with a single duct; *g*, more highly differentiated alveolar glands, with compound ducts. (Modified from Wilder.)

corium, thus adding enormously to the total secreting area, just as large bays and inlets increase greatly the actual extent of a coast line.

Many-celled epidermal glands, which occur higher up the scale in land forms, are either *tubular* or *alveolar* (Fig. 137). Each of these kinds may be either simple, or branched and compound. The amount of space such a gland occupies at the surface is relatively small, being simply a tiny pore for the escape of the secretion.

B. Invertebrate Glands

Representatives from nearly every phylum of the invertebrates exhibit integumentary glands that serve a variety of purposes.

The *Cnidaria* among the cœlenterates receive their name from the widespread occurrence of characteristic, glandular, stinging cells (*nematocysts*) in the ectoderm, by means of which small prey are paralyzed, and the attacks of enemies probably warded off. *Rhabdites*, small rodlike bodies found in certain worms, are secreted apparently for a similar purpose.

Sedentary animals frequently gain anchorage by glandular activity. Thus, the *cement glands* of barnacles enable these curious cousins of the crabs to stand on their heads securely fastened within their protective shells, in which position they can tranquilly kick food into their mouths in safety. Many molluscs also, certain mussels, for example, by the secretion of byssal threads from a *byssal gland*, attach themselves to some solid foundation. Even microscopic rotifers, as they inch themselves along, manipulate their tiny bodies by the aid of a sticky "*tail gland*," while the lacquered cocoon in which an earthworm deposits its underground eggs, is secreted by the glandular *clitellum*.

Many insects produce glandular secretions. The defensive odor of stink bugs, the protective millinery of woolly aphids, the poisoning power of myriapods, spiders, and brown-tailed moths, as well as the spinning of caterpillars and spiders, are all due to hypodermal glands, while anyone who has ever picked up a fat-bodied blister beetle (*Meloë*) will remember the acrid, yellow "elbow grease" that exudes glandular unfriendliness from its joints.

C. Vertebrate Glands

1. *Fishes*

The almost universal epidermal glands of fishes are superficial one-celled *mucous glands*, which are widespread over the surface of the scales, and wherever naked skin occurs. They are supplemented by two other kinds of glandular cells, namely, *granular gland cells*, which are especially abundant throughout the epidermis of cyclostomes (Fig. 129), and the more deeply lying, enlarged, *beaker cells* that frequently extend from the Malpighian layer all the way to the surface. All three of these kinds of glands combine to render fishes slippery and hard to grasp. Doubtless too they effect the constant removal of foreign substances that may adhere to the body, and by lubrication facilitate, to a certain extent, the passage of these submarines through the water.

The African lungfish, *Protopterus*, has skin glands that produce a varnish-like cocoon in which it æstivates, buried in the mud, and thus survives the dry season.

The *pterygopodial glands*, associated with the pelvic "claspers" of male dogfish and other selachians, are pluricellular, mucous glands that have to do with copulation.

Deep-sea fishes that live in a world of darkness where no ray of sunlight can penetrate are, in many instances, equipped with glandular, integumentary organs of considerable complexity, that produce phosphorescent light. These *light-producing glands* (Fig. 138), which are the only many-celled glands in the skin of fishes, are usually accompanied in those species possessing them by enormously developed eyes, adapted to catching the faintest glimmer of phosphorescence. Thus, when Diogenes of the Deep

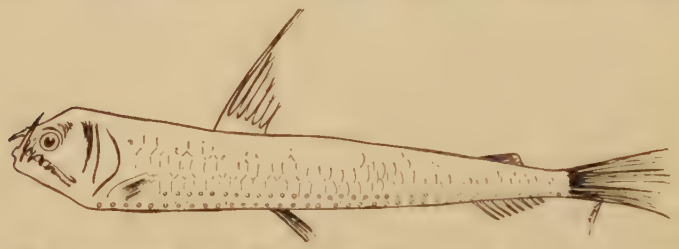


FIG. 138.—A deep-sea teleost, *Chauliodus*, with a double row of phosphorescent light organs on either side. (After Lendenfeld.)

Sea fares forth, his lantern may not pass by unnoticed. Other deep-sea fishes, without light-producing organs, are usually entirely blind or with very degenerate eyes.

2. Amphibians

With the exception of the so-called *Leydig's glands* that occur in the larvæ of some urodeles, one-celled epidermal glands, so characteristic of the fish skin, do not appear in the amphibians, but are replaced by many-celled alveolar glands. Still higher up among land forms that come into contact with dry air, the epidermal mucous glands which typically cover the outside of a wet fish, have retreated from the surface of the body to internal passages, such as the nose and mouth, where they give character to the "mucous membrane."

One of the functions of the skin glands of fishes and amphibians, which does not recur as an integumental activity in higher verte-

brates, is the production of irritating or poisonous substances as a means of protection against enemies. In fishes such *poison glands* are usually associated with puncturing spines, or sharp fin rays, but in amphibians they are more generally distributed over the body. Toads, for example, have few enemies, on account of the noxious secretions from their skin glands, and the glandular rings that alternate with the tiny embedded scales of the blind cæcilians (Apoda), are equipped not only with many-celled mucous glands, characteristic of amphibians, but also with *giant poison glands* (Fig. 133).

Fig. 139.—Hind foot of a tree frog, showing glandular sucking discs at the ends of the toes. (From Hilzheimer, after Dollo.)

Another function of ectodermal glands is peculiar to tree frogs (Fig. 139) and certain salamanders, namely, *glandular feet* that enable them to stick to vertical surfaces. Again, some male frogs find a unique use for glands in their swollen thumbs that enable them at breeding time to hang to the backs of the females upon which they are saddled, until the extrusion of the sperm and eggs (Fig. 392).

3. Reptiles and Birds

Epidermal glands are much reduced in reptiles and birds, but whenever they do appear are quite localized. For example, down the back of an alligator from neck to tail there is a row of crowded degenerate glands between the first and second row of scales on either side of the mid line, the use of which is unknown. On the under side of the lower jaw also there is a pair of evertible structures usually regarded as glands that, at times, give forth a musky odor, and probably have something to do with the sex psychology of these animals. Similar *odoriferous glands* occur in other reptiles. They are a most notable possession, for example, of the "stinkpot" turtle whose scientific name, *Aromochelys odorata*, is almost as descriptive as its common name, and are particularly localized about the cloacal opening of certain snakes.

The so-called *femoral "glands"* of male lizards, extending along the inside of the hind legs from knee to cloaca like a row of tiny portholes (Fig. 140), produce a dry, gummy secretion which hardens into short spines, or "teeth" (Fig. 141), that are useful as a gripping device during copulation.

The *uropygial* or *preening glands* are best developed in water birds, and are said to be odoriferous during sexual activity, which suggests that their ancestral function was sex allurement, although their chief use has now come to be that of supplying oil for preening the feathers. They are paired structures, usually with a single outlet. In ducks and pelicans there are several ducts present. Aside from the uropygial gland at the base of the tail,

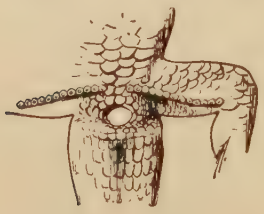


FIG. 140. — Femoral "pores" of male *Lacerta*, probably useful in grasping the female during copulation. (After Maurer.)

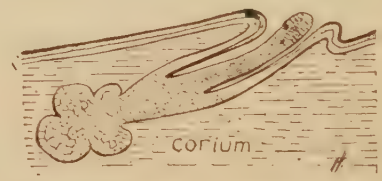


FIG. 141.—Section through a single femoral pore (Fig. 140) of a lizard, *Lacerta*, showing projecting plug of dry cells that may help to prevent slipping during copulation. (After Bütschli.)

the only other integumental glands in birds are certain oily glands in the external ear passage of some gallinaceous birds, like the European capercaillie (*Tetrao urogallus*), and the American turkey.

4. Mammals

Integumental glands reach their greatest variety and differentiation in the mammalian skin. None of them are unicellular. The more important are of either tubular or alveolar structure.

a. TUBULAR GLANDS

Sweat glands are the most common and generally distributed of the tubular glands. Dr. Oliver Wendell Holmes, in his lectures to Harvard medical students, likened sweat glands to "fairies' intestines." Each one is an elongated tube, the walls of which are composed of cells (Fig. 142). The deeper glandular portion is usually coiled up to occupy less space, while the outermost part, that serves as a duct and opens at the surface with a funnel-shaped pore, often spirals like a corkscrew, as if it found difficulty in penetrating the compact outer corneal layer of the skin. Although originating, like all other integumentary glands of vertebrates, in the epidermis, sweat glands by a process of growth push deep down into the corium where their terminal glandular part comes

into intimate contact with the capillaries, making possible the extraction of sweat from the blood. In a healthy man this fluid, visible and invisible, amounts to a daily loss of from one to five pints, or in some cases to as much as 2% of the entire body weight.

It is literally true that a man "sweats blood," for sweat is derived from that source of supply. The sweat of the hippopotamus, as well as of the giant kangaroo (*Macropus rufus*), is actually reddish in color, resembling blood. That of the African antelope, (*Cephalopus*), is said to be bluish in color, and contains some albuminous component which may cause a lather, as is also true in the well-known case of an overheated horse.

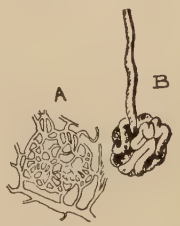


FIG. 142.—A sweat gland. *A*, a network of capillaries inside of which lies the coiled end of a sweat gland, *B*. (After Kimber.)

Sweat glands are wanting in *Echidna*, some insectivores, *Chrysochloris* and *Talpa*, the scaly anteater, *Manis*, the two-toed sloth, *Cholepus*, and the sirenia and cetacea which live in water.

It has been estimated that there are two and one-half million sweat tubules in the human skin, each with a separate pore just at the limit of visibility to the naked eye. They are not equally distributed being more numerous on the palms and soles than elsewhere, and attaining a notably greater size under the armpits. Certain racial differences in the abundance of sweat glands have also been noted, as shown by the following counts per square centimeter on the finger tips: American soldier, 558; Filipino, 653; Negrito, 709; Hindu, 738.[1]

In mammals that are abundantly clothed with hair, the sweat glands become crowded out or localized. Thus, in cats, rats, and mice, these glands are confined to the soles of the feet; in bats, to the sides of the head; in rabbits, to an area around the lips; in deer, to the region around the base of the tail; in shrews, to a line down either side of the body; in ruminants, to the muzzle and the skin between the toes; while in the hippopotamus sweat glands appear only on the ears, which are the parts of the body of these semi-aquatic monsters most exposed to air.

In closing this brief resumé of mammalian sweat glands it may be added that the moist muzzle of cattle, sheep, goats, pigs, dogs, and cats, is due to the presence of modified sweat glands;

[1] *Anat. Rec.*, 1917, 1.

while the uncoiled *ciliary glands of Moll* at the base of the eyelashes in man, that are the center of trouble whenever a "sty" is formed, are likewise modified tubular glands.

b. ALVEOLAR GLANDS

While tubular glands are confined to mammals, alveolar glands of various kinds occur not only in the mammalian skin but also in the skin of other land vertebrates, as has already been noted.

The most universally distributed of the mammalian alveolar glands are the *sebaceous glands* which produce an oily secretion (*sebum*), usually in connection with hairs (Fig. 190), although they are found independent of hairs at the edge of the lips and about the genitalia, where the skin passes over into the mucous membrane. On the tip of the nose, particularly the bulbous middle-aged type, the openings of free sebaceous glands may be seen as tiny pits, marking the locality of ancestral hairs that have been lost in the evolutionary shuffle.

Sebaceous hair glands may be two or three to each hair, opening into the pocket from which the hair shaft projects, rather than directly upon the surface. The size of the sebaceous glands is not in relative proportion to the size of the hairs with which they are associated, and they frequently become enlarged in the absence of hairs, which suggests that their primary function is not so much concerned with oiling the hair, as is commonly thought, as with coating the surface of the skin itself with oil.

The two-toed sloth, *Cholepus*, the Cape mole of South Africa, *Chrysochloris*, the scaly anteater, *Manis*, and the water-inhabiting sirenia and cetacea, already cited for their lack of sweat glands, are equally deficient in sebaceous glands, although the first two are abundantly hairy animals.

Along the edge of the eyelids is a line of modified sebaceous glands, not to be confused with the "ciliary glands of Moll," called the *Meibomian glands* (Fig. 680), which produce an oily film across the eyeball between the edges of the eyelid and the eyeball itself, that retreats and advances with every wink. This oil seal normally retains the film of tears that constantly moistens the eyeball, but, in the case of a weeping child, for example, the oily dam is broken by the flood pressing from behind, and the tears fall out of the eyes.

Another type of integumental alveolar glands occurring in various mammals are those associated with sexual activity. They

should not be confused in any way with the so-called primary sex "glands" which produce eggs and sperm. They are derivatives of the epidermis and may have a lubricating function in connection with the genital organs, as, for example, the *preputial*, and *vulvo-vaginal glands*, or they may be *scent glands*, which act as an allurement to the opposite sex. Scent glands are usually located near the anus, as in the musk deer, civet cat, dog, fox, and skunk.

In the external ear passages of most vertebrates are to be found the *ceruminous*, or *wax glands*, which in form show affinities with the tubular type, but in function are more like the sebaceous glands, since they produce a gummy, waxy secretion more like oil than sweat. They serve to arrest dust particles, and to discourage adventurous insects that might be tempted to invade the sacred precincts of the ear. This latter function is not so apparently needful in the case of man as of a dog sleeping in the sunshine with a halo of busy insects around its head.

c. MAMMARY ORGANS

Of paramount importance in the life scheme of mammals are the *milk glands* which characterize this order of animals. The mammary glands, although resembling the necrobiotic sebaceous glands in structure, are "vitally secretory" in function, like the tubular sweat glands. They are in all probability not derived from either sweat or sebaceous glands, but from some common ancestral type less differentiated than either. Their activity, however, is periodic instead of continuous and, for the most part, finds expression only in the female.

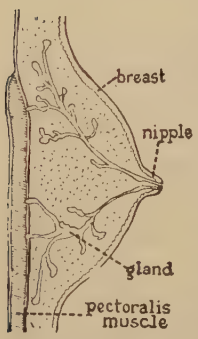


FIG. 143.—Sagittal section of the mammary gland through the nipple. (After Radasch.)

FIG. 144. — Arrangement of nipples in *Didelphys henseli*. (From Weber, after O. Thomas.)

The mammary apparatus includes not only the *mammary glands* themselves, but also the elevated *nipples*, that furnish outlet for the glands, and the *breasts*, or "mammæ," which are integumental swellings produced by the localized presence of the mammary glands in the skin (Fig. 143).

The *number of nipples* varies from two in the horse, bat, whale, elephant, and man, to twenty-five in the opossum (*Didelphys henseli*, Fig. 144). Carnivores usually have six to eight; rodents, two to ten; pigs, eight to ten; and ruminants, four. In those species where several young are born in a litter, there is a corresponding provision in the number of nipples.

The *number of ducts per nipple* that drain the glands, is also subject to considerable variation. In mice, ruminants, and insectivores, there is only one. The pig has two or three; carnivores, three to six; and in man there is a cluster of about twenty separate ducts opening into each nipple.

Milk, which is secreted by these glands, is the natural food of young mammals. It is composed of water, derived from the blood stream, butter-fat, milk sugar, albumin, and certain salts in varying proportions in different species of mammals, as indicated by the analysis of von Bunge in the accompanying table.

	Albumin	Fat	Milk Sugar	Ash
Man	1.6	3.4	6.1	0.2
Dog	7.3	11.9	3.2	1.3
Cat	7.0	4.8	4.8	1.0
Guinea pig	10.4	16.7	2.0	2.5
Pig	5.1	7.7	3.3	0.8
Horse	2.0	1.2	5.7	0.4
Cow	3.5	3.7	4.9	0.7
Goat	3.7	4.3	3.6	0.8
Sheep	4.9	9.3	5.0	0.8
Reindeer	10.4	17.2	2.8	1.5
Camel	4.0	3.1	5.6	0.8
Llama	3.9	3.1	5.6	0.8
Dolphin	7.6	43.8	—	0.5

It will be noted that albumin in milk favors rapid growth in the young. A guinea pig, whose milk contains approximately ten per cent of albumin, doubles its weight after birth in six days, while the human infant, feeding upon milk with less than two per cent of albumin, requires 180 days in which to double its weight. Of course other factors than the food factor enter into this difference in growth, but the fact remains that different kinds of milk are adapted in nature to different requirements. Where selective breeding for milk production has been practiced for a long time, as in domestic cattle, it is not unusual to find a cow which, in a

single year, can produce fifteen times her own weight in milk. There is thus an enormous potential output from these secretory glands.

Mammary glands may develop almost anywhere in the mammalian skin, as shown by instances recorded in medical literature of the abnormal occurrence in human beings of mammæ even under the armpits, on the shoulders, or upon the hips. Their normal distribution in different species of mammals, however, holds a definite relation to the accessibility of the nipples to the sucking young. Thus, in carnivores and swine, which attend to their nurslings while lying down, the nipples are arranged in two rows down the ventral sides. Quadrupeds that, in contrast to carnivores and swine, stand habitually upon underpinning legs, have their nipples in a protected situation between the legs, either anterior, as in elephants, or posterior, as in cattle and horses. Arboreal animals that hold their "babes in arms," have convenient pectoral nipples. Man, with a probable arboreal ancestry, also has pectoral nipples. The grotesque sea cows, which enfold their single offspring with their flippers and "stand" in water with head projecting in air, likewise have pectoral nipples. This circumstance has no doubt contributed to the "mermaid" myths about sea cows among sailors. The baby whale (Fig. 145), unlike the young of the sea cow, is a "trailer," since the mother's nipples are situated far posterior on either side of the sexual orifice in pockets which fit over its snout, thus minimizing the amount of salt water that is liable to become mixed with the milk of these marine infants that suck while navigating the high seas. The opposite extreme in the position of the nipples is found in the topsy-turvy bats and flying lemurs (Fig. 146), whose offspring

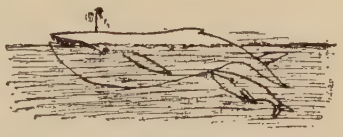


Fig. 145.—Humpback whale suckling her young. (From Buckley, after Scammon.)

Fig. 146. — The flying lemur. *Galeopithecus*, "whose offspring literally cling for dear life to the breasts of their floppy mothers" (After Hilzheimer.)

literally "cling for dear life" to the breasts of their floppy mothers, the accessible nipples of which are axillary in location, or under the armpits.

The *development of the mammary apparatus* is initiated by the formation of an epidermal ridge down either side of the belly from axilla to groin. This is called the *milk-line stage* (Fig. 147), and it occurs in man near the beginning of the second fetal month when the embryo is still less than half an inch in length. The milk-line stage is succeeded by the *milk-hill stage* (Fig. 148), which results when the epidermal ridge becomes absorbed except for a beadlike row of remnants. Each one of these epidermal "beads," or "hills," marks the possible location of a future mammary gland. The tiny milk hills are compact masses of cells which later sink into the underlying tissue, no longer leaving any external trace of the mammary apparatus, except a double row of depressed "hills" embedded in the corium. This is called the *milk-field stage*. As the leveled hills of the milk-field stage sink still deeper and become valleys, there is formed a double row of pits along the belly wall, converging from the anterior posteriorly and representing the *milk-pocket stage* (Fig. 149). The cells that form the sides and bottom of these milk pockets give rise to the mammary glands. In those forms that do not have two complete rows of nipples, certain pockets fail to develop. In man it is the fourth pair of embryonic milk pockets from the anterior end, that become the permanent mammæ. The final differentiation of the mammary apparatus takes place when the milk-pocket stage is succeeded by the *nipple stage*.

Fig. 147. — The milk line in a pig embryo of 1.5 cm. (After O. Schultze.)

Fig. 148. — Milk-hill stage in a pig embryo of 1.9 cm. (After O. Schultze.)

There are two ways in which nipples form, resulting in what are distinguished as *true*, and *false nipples*. In the formation of true nipples, as in rodents, marsupials and primates, the floor of the milk pocket, into which the ducts of the mammary glands open, elevates, carrying the ducts of the milk glands with it, thus causing them to open at the tips of the nipples. In the case of false nipples, on the con-

trary, which characterize carnivores, pigs, horses, and ruminants, the floor of the milk pocket with its ducts remains unelevated, while the margins of the pocket pull up to form the nipple. There is thus formed a secondary tube, or extension upward of the milk pocket itself, called the *milk canal,* into which the mammary glands pour their secretion, to be carried to the tip of the false nipple.

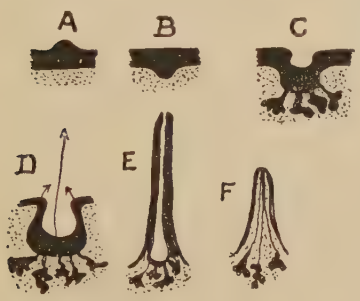


Fig. 149. — Development of the mammary glands. *A,* diagrammatic cross section through the milk line (Fig. 147); *B,* the epidermal milk line, after breaking up into a chain of isolated milk hills (Fig. 148) has sunk down into the corium (dotted) and is no longer apparent externally, thus forming the milk-field stage; the levelled area, where the milk hills were, becomes depressed, *C,* forming the milk-pocket stage. The sunken epidermal plug penetrates still deeper into the corium, giving rise to the mammary glands. *D,* preliminary indifferent milk-pocket stage, with the two short arrows indicating the direction of epidermal growth that results in the formation of a "false nipple," while the long arrow shows how the "true nipple" forms; *E,* false nipple, with ducts of the mammary gland opening at the bottom of a milk canal; *F,* true nipple, with the mammary ducts opening directly at the tip.

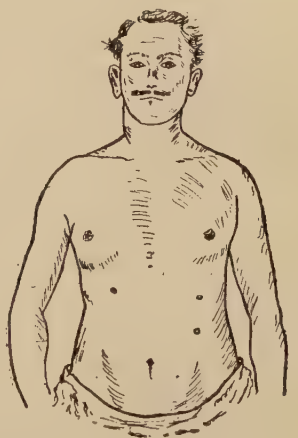


Fig. 150. — Hyperthelism. Three supernumerary mammæ are shown. (From Martin, after a photograph by Mollison.)

The mammary apparatus develops equally in both sexes up to the time of puberty, when it degenerates in the male and becomes potentially functional in the female. The male may produce milk, as in the monotreme, *Echidna,* and in exceptional instances among higher mammals, even in man. Such abnormal behavior is termed *gynecomastism.*

In man as well as in other mammals, there is not infrequent occurrence of extra nipples, *hyperthelism* (Fig. 150), or extra breasts, *hypermastism* (Fig. 151). Such persistent embryonic relics, particularly in the case of hyperthelism, occur quite as

frequently in males as females. Supernumerary nipples usually arrange themselves along the vanished embryonic milk line.

The mammary apparatus of *Monotremes* presents many exceptions to that of other mammals. The glands are branched-tubular in form instead of alveolar, and produce a sort of nutritious sweat instead of the usual milk (Fig. 152). No nipples are present, tufts of hair serving in their stead. The young monotreme does not have muscular lips and, handicapped with a horny beak, is quite unable to suck, so it licks the nutritious sweat from the makeshift tufts of hair with its protrusible tongue. The skin on the belly of *Echidna* forms a temporary pouch, or *incubatorium*, that surrounds the mammary area. Into this pouch is deposited the leathery-shelled egg, that soon hatches into a very helpless embryo, there to undergo the preliminary perils of early development which other mammals accomplish more safely within the protective uterus of the mother. In *Ornithorhynchus* there is not even an incubatorium present. It is thought that the egg is brooded in a hole in the ground which serves as a nest. The mammary area is depressed, as in the milk-pocket stage, opening through a slit in which tufts of hair that serve as nipples, project. Probably gynecomastism occurs in *Ornithorhynchus*, as well as in *Echidna*, and both parents share in feeding the young.

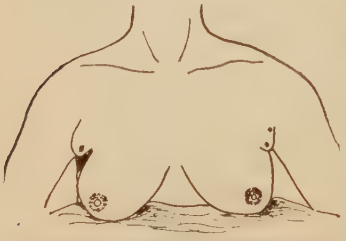


FIG. 151.—A case of hypermastism. (After Hansemann.)

FIG. 152.—Ventral view of *Echidna*, with the skin loosened on one side to show the mammary glands. (After Semon.)

Most *Marsupials* in connection with the mammary apparatus regularly possess a pouch for carrying the immature young (Fig. 16, E). True nipples are present within the pouch and typical milk glands supply real milk. The nipples project, however, only during lactation. At other times they retract, like a disappearing gun, within the surrounding pit in the skin. The young marsupial

retains its hold upon the nipple by means of powerful sphincter muscles around its own mouth, and the enveloping edge of the marsupial pocket that surrounds the nipple (Fig. 153). At first it is so helpless that it is necessary for the mother to pump the milk down its waiting throat by means of the contraction of the breast muscles. Later, as it learns to handle its own nerves and muscles, the little marsupial becomes able to feed itself.

Fig. 153.—A young marsupial, *Sminthopis*, with its snout gripped by the cuplike marsupial pocket, and the nipple (represented in black) crowded far down the throat. (After Bresslau.)

In placental mammals the marsupial pouch disappears, since the fetus is cradled in greater safety within the uterus until, at birth, a stage of development has been reached that makes bodily protection on the part of the mother less imperative. There are certain dim reminders of a marsupial pocket around the nipple, however, even in the human embryo, for, at about the beginning of the second fetal month when the future mammary apparatus is being initiated, there develops around the milk hills transitory epithelial thickenings that possibly represent the last remnants of an ancestral marsupium (Fig. 154).

Fig. 154.—Reconstruction of transitory epithelial structures around the mammary glands in the skin of a human fetus 56 days old . The dotted circles represent the area where the budding arms joined the body. The two large black dots are the epidermal "milk hills" that are to give rise to the mammary glands, and which locate the position of the future nipples. The twenty-one smaller black dots are epithelial thickenings around the nipples, which may be the vanishing remains of ancestral marsupial pockets. (From Walter, in Anat. Anz. XXII, 1902.)

The prolonged obligatory period of milk feeding among the higher mammals, which allows time for a more elaborated development and is the necessary preliminary to the *process of learning* through association with the parents, is a very fortunate condition of life, that has gone far in helping the dominant mammals to work out their salvation.

2. Hard Integumentary Structures

A. Scales

1. Fishes

While every class of vertebrates, except cyclostomes, has some representatives with a scaly skin, the presence of scales may be regarded as the most notable modification of the integument of fishes and reptiles. Whenever fishes occur lacking scales, as in the case of eels and certain bottom-feeding forms, it is to be regarded as a secondary modification and not the primary ancestral condition, since in embryonic eels scales are present.

Fig. 155.—A restoration of an armored Ostracoderm *Pterichthys*, from the Devonian in Scotland. (After Traquair.)

There are at least four types of fish scales of particular interest to the comparative anatomist, namely, *placoid*, *ganoid*, *cycloid*, and *ctenoid*, not including bony dermal plates that reached a high degree of elaboration in the extinct *Ostracoderms* (Fig. 155), and other armored fishes of early geologic times.

a. PLACOID SCALES

The most primitive scales are *placoid*, appearing first in the ancestral sharks (*Cladoselachia*) of the Upper Devonian, and found in selachians generally. In structure a placoid scale consists of a flat, basal plate embedded in the skin, usually carrying a spiny projection of dentine capped with hard enamel like a tooth. The transition in structure and position from the placoid scales of the skin on the outside of the head, to the rows of teeth within the margin of a shark's jaw is so continuous and unmistakable that teeth may be regarded simply as modified placoid scales (Fig. 156). The basal plate of the scale corresponds to the cement layer of the tooth, while the projection of dentine and its enamel cap are quite like familiar similar parts of a typical tooth.

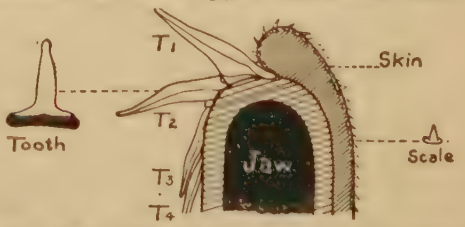


Fig. 156.—Diagram of the edge of a shark's jaw, to show the relation of placoid scales and teeth. T_1, tooth in service at the edge of the jaw; T_2, T_3, T_4, reserve teeth. (Drawn by K. L. Burdon.)

Placoid scales in dogfishes and sharks are usually small and closely set without actually overlapping, although their backward projecting spines aid in effecting protection of the tiny spaces of bare skin between the embedded scales. In skates and rays the placoid scales, which may be quite large with jagged spines, are often localized in certain exposed areas, as down the median line of the back, leaving scaleless patches of the skin exposed.

b. GANOID SCALES

The few kinds of ganoid fishes living in fresh waters today are the last survivors of a large diversified order which ruled the Devonian seas. Their scales present a variety of form and structure out of all proportion to the number of species involved. In the sturgeon, *Acipenser*, for example, they are large, isolated, bony scutes, not entirely covering the skin but located in exposed situations where there is the greatest wear and tear, like the rows of brass-headed nails decorating the edges of great-grandfather's chest. In the garpike, *Lepisosteus* (Fig. 157), as well as in the related forms, *Calamoichthys* and *Polypterus*, the scales are hard, polished, rhombic plates, fitting edge to edge or very slightly imbricated one over the other, thus forming a complete armor, while in the bowfin, *Amia*, they overlap, after the more modern fashion of the bony fishes. In all these ganoids except *Amia*, however, the outside surface of the scales is composed of *ganoin*, a hard substance secreted by the corium and susceptible of high polish, which is not at all homologous with the ectodermal enamel that caps placoid scales. There is some embryonic evidence (Tims, 1905), that a ganoid scale is to be compared to several placoid scales mounted upon a single basal plate. The skin of the spoonbill sturgeon, *Polyodon*, is almost completely without scales. In fossil ganoids, scales were frequently quite large and platelike, and even in living survivors those that cover the head may become enlarged dermal scutes, which take part in the formation of the investing bones of the skull.

FIG. 157.—Ganoid scales of *Lepisosteus*. Three of them are perforated with openings to the lateral line organs.

c. CYCLOID AND CTENOID SCALES

The great majority of modern fishes, that is, the *teleosts*, have either cycloid or ctenoid scales, when any are present.

Cycloid scales, as the name indicates, are rounded in shape (Fig. 158), and thicker in the center, thinning out toward the margin. If such scales were spread over the surface, edge to edge like ganoid scales, they would much more than cover the body. They are, however, embedded in the corium with only the outer margin exposed. Consequently they project diagonally at an acute angle with the surface of the skin, and overlap their neighbors like shingles, so that the entire body is protected by at least a double thickness of scaly armor at every point.

FIG. 158.—Cycloid scale of a salmon showing lines of growth. (After Hesse.)

Ctenoid (comblike) scales are also rounded in form, but with a toothed edge in addition along the margin which is embedded in the skin (Fig. 159). This toothed, or serrated, edge fastens the scale more securely in place, so that it is much more difficult to loosen and remove ctenoid than cycloid scales.

Of these two types the cycloid scale is the more primitive, occurring first in the Jurassic Period, while the ctenoid type did not appear until Cretaceous times. Moreover, the ctenoid type in development passes through the cycloid phase, as would be expected in light of its succession in geologic time. All intermediate stages between the cycloid and ctenoid types are to be found. In some fishes as, for example certain flounders, the scales on the upper side are ctenoid, while those on the under side are cycloid.

FIG. 159.—Ctenoid scale. (After O. Hertwig.)

Both cycloid and ctenoid scales are entirely dermal in their origin. The *scleroblasts*, or scale-forming cells in the corium, lay down two layers of different substance in the formation of a scale. The outer layer is homogeneous and bony, while the under one is fibrillar and contains calcareous deposits. Such a scale increases in thickness and area by the activity of the scleroblasts, and successive additions are indicated by lines of growth like the similar rings of wood exhibited on the trunk of a tree. Inasmuch as periods

of growth alternate with periods of comparative inactivity with most fishes according to the seasonal variation in their food supply, it is possible to estimate the relative age of a fish by an examination of the diary-like lines on its scales. In addition to the marginal lines of growth, certain radial grooves are also present, caused by the failure of the outer homogeneous layer of the scale to be deposited in these places. Radial grooves add somewhat to the flexibility of scales, a very desirable device since teleost scales, although thinner than the tilelike ganoid type, by reason of shingling, form a double envelope over the underlying muscles that tends to hamper free movement. Some teleost fishes, as the pipefish, *Sygnathus*, and the curious sea horse, *Hippocampus*, do not have overlapping scales but are encased in a cuirass of bony plates. In the lungfish, *Neoceratodus*, the large thin oval scales superficially resemble the cycloid scales of teleosts, but in reality are of different texture and have a different manner of development.

2. Amphibians

In modern amphibians scales are absent, with the exception of the tiny bands of embedded scutes in the skin of the tropical, legless cæcilians. The *Stegocephali*, an extinct group resembling amphibians, that flourished in the Devonian times, were characterized by bony plates in the skin particularly on the ventral side, but it is doubtful whether these problematical animals should be reckoned as the ancestors of true amphibians, whose fossil remains do not begin to appear until the Carboniferous Period, some time after the last of the Stegocephali had vanished.

3. Reptiles

Reptiles, like ganoids, are represented today by a few divergent, specialized types,—lizards, turtles, snakes, and alligators,—superficially quite unlike each other, which have survived to tell the tale of the vast age-long experiment in reptilian creation.

So far as scales are concerned these survivors agree in the predominant part that the epidermis plays in their formation. Small bony plates, or *ossicles*, of dermal origin are present, sunken in the skin and spaced with much regularity. They are covered, however, by a continuous layer of epidermis in which the corneal layer becomes thickened or embossed wherever it covers an ossicle, while it is thinner and more flexible between the plates

(Fig. 160). Thus, reptilian "scales" hang together as a continuous armor and cannot be scraped loose, as may the separate independent scales of teleost fishes.

This entire, dry, corneal layer of skin in the case of snakes, periodically loosens and is cast off. Such is not the procedure with turtles and alligators, for in these animals the corneal scales that overspread the dermal plates in the skin, are discontinuous, and the demands of increasing size are met by concentric, marginal lines of growth which are added to each scale. The highest development of the bony underpinning of dermal scales is reached in the turtles, although some of the extinct dinosaurs were fearfully and wonderfully made in this particular. Many reptiles like the "horned toad," *Phrynosoma*, as well as alligators and crocodiles, exhibit spines or embossed patterns on the epidermal

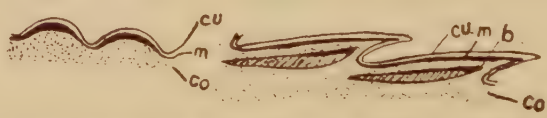


FIG. 160.—Diagrammatic long section through reptilian scales. *b*, bony dermal plate embedded in corium; *cu*, corneal layer, forming the continuous external scales; *co*, corium; *m*, Malpighian layer. (After Boaz.)

scales, while the rasplike character of the ventral scales on a snake's body serves in obtaining a frictional grip on the ground over which these animals glide. The head of a snake, which has to poke about between obstacles, is ensheathed in enlarged platelike scales, while the sense of touch, which thereby becomes inoperative over the surface of the head, is transferred to the delicate, protrusible tongue.

4. Birds

There is very little to say about the scales in a bird's skin, since aviation has no use for such heavy clumsy structures. Only on such unfeathered areas as the shanks and around the base of the beak, is the epidermis thickened and cornified into a semblance of reptilian scales, and nowhere in a bird's skin do dermal ossicles occur.

5. Mammals

Scales, although generally replaced by hairs in mammals, still persist in a number of instances. They are large, horny, and imbricated in the scaly anteater, *Manis*, being shed and renewed

singly. In the armadillos no ecdysis occurs, but growth is accommodated within the shieldlike armor by marginal accretion of the separate elements, as in turtles. A great variety of mammals have scaly tails, for example, the beaver, rat, mouse, opossum, mole, shrew, and certain lemurs. Scales occur on the back of the paws of moles and shrews, and even the fetus of the brown bear, as already mentioned, testifies to some sort of a scaly past by developing transient, useless, embryonic scales over the back. There is little to show that mammalian scales are derived either from the separate dermal scales of fishes, or the continuous epidermal thickenings of reptiles. Such structures of unknown derivation are termed *neomorphs*.

B. Horns

Horns are in part integumentary structures. The earliest known horns appeared as bony projections on the heads of certain ceratopsid dinosaurs (Fig. 36). It is probable that these bony projections were surrounded by horny sheaths, although positive evidence is not furnished by the fossils themselves. Among modern reptiles there are a few bizarre lizards with horns, for example, *Chameleon oweni*, and *Ceratophora stoddærti* (Fig. 161). Otherwise horns are to be found today exclusively on hoofed mammals. There are four general kinds, namely, keratin-fiber horns, antlers, pronghorns, and hollow horns.

Fig. 161.—Head of a male lizard, *Ceratophora stoddærti*, with a horn on its snout. (After Darwin.)

1. Keratin-Fiber Horns

Horns of this type are made up of hairlike keratin fibers, cemented together into a hard, compact mass. They are entirely epidermal and have no bony core. The Indian rhinoceros carries one of these horns on its "nose," as its name indicates, and the African rhinoceros has two, arranged tandem fashion rather than in the conventional way of paired structures. It is said that *Bos triceros*, one of the kinds of native cattle of Africa, also sports horns of this curious type.

2. Antlers

Antlers are commonly borne by the various representatives of the prolific and diversified deer family (*Cervidæ*), ordinarily only by the males, but by both sexes in case of the reindeer, *Rangifer*.

They consist of skeletal outgrowths from the skull, which at first are covered over by the hairy skin. While in that condition a stag is said to be "in velvet" (Fig. 162). Later the skin dries

FIG. 162.—The growth of antlers. *A*, April 2; *B*, April 20. (From Stone and Cram.)

and becomes rubbed off, leaving the antlers as unadorned bone, when of course it is incorrect to include them among integumental structures. At the end of the second year, sometime before the mating season, the single-pronged antlers weaken at the base next the skull by the breaking down of some of the bony tissue, and are broken off. The surrounding skin grows over the wounds thus made, and a new pair of antlers "in velvet" grows out (Fig. 163), this time with two prongs

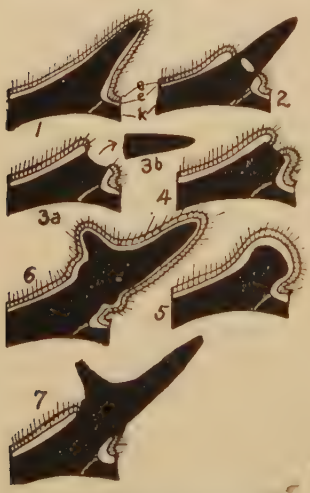


FIG. 163.—Diagrams showing how antlers are shed. (After Nitsche.)

FIG. 164.—Big antlers of a moose. (After Stone and Cram.)

instead of one. Thereafter each successive breeding season for some time is celebrated by new antlers usually with an additional prong on each (Fig. 164). The shedding and renewal of antlers does not occur in castrated bucks.

That "fantastic deer," the giraffe, has a pair of short, single antlers that are permanent, and remain in velvet throughout life. The lateral prongs of the antlers of reindeer are greatly flattened, so that they serve as snowshovels to aid these Arctic dwellers in getting at the buried mosses on which they feed in winter.

3. Pronghorns

The pronghorn antelope, *Antilocapra americana* (Fig. 165), and the "saiga" antelope, *Saiga tatarica*, possess permanent antlers, of which the thimble-like sheath of horny integument is periodically shed and renewed, without the loss of the bony core.

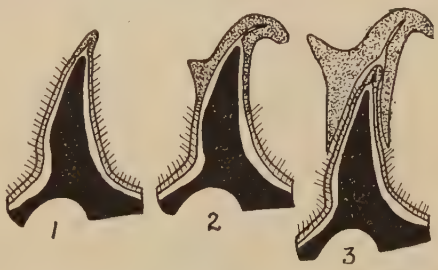


Fig. 165.—Antler formation in the pronghorn antelope, *Antilocapra*. *1*, appearance shortly after shedding the antlers; *2*, later stage, with a new epidermal "thimble" forming with an extra prong; *3*, old antler tip ready to be cast off, with new thimble already formed within. The bony core of the antlers is represented in black. (After Nitsche.)

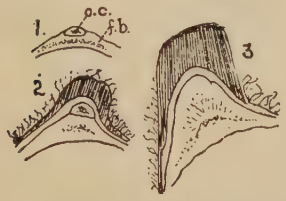


Fig. 166.—Three stages in the formation of a hollow horn of a young lamb. *1*, frontal bone with the *os cornu*, *os*, or bony core of the horn appearing; *2*, horny thickening over the *os cornu* beginning to be formed; *3*, the hollow horn definitely established and the *os cornu* fused with the frontal bone of the skull. (After Brandt.)

4. Hollow Horns

Perhaps the most familiar kinds of horns are the hollow horns of domestic and wild cattle, sheep, goats, and antelopes, which are usually present in both sexes. These are strictly epidermal structures that are not shed as is the case with the pronghorns. As the horn wears away it is renewed from the Malpighian layer of the epidermis, just as any other dead, corneal structure. The hollow horn fits over a core of living bone, that is attached to the frontal region of the skull (Fig 166). Hollow horns do not branch, like antlers, but they assume a great variety of form all the way from the majestic graceful spread in a Texas steer to that of the "cow with a crumpled horn."

C. Digital Tips

With the exception of the Amphibia, the tips of the digits, in those vertebrates that have fingers and toes, are reinforced by hard integumentary structures, either *claws*, *nails*, or *hoofs*. Although amphibians do not have true claws, a thickening of the corneal layer of the epidermis at the ends of the fingers and toes is a prophecy of the claws to come later in the vertebrate series. In the African toad, *Xenopus*, and a Japanese salamander, *Onychodactylus*, these epidermal thickenings assume the definiteness of actual claws on some of the digits.

1. Claws of Reptiles

The typical claw of a reptile (Fig. 167, 1), may be regarded as being made up of two scalelike, horny plates, dorsal and ventral,

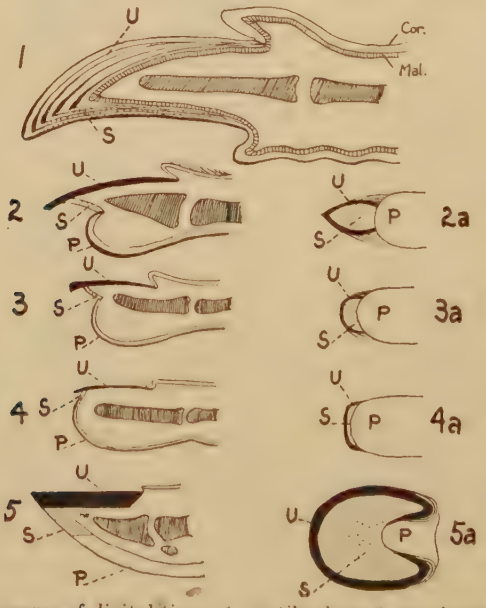


Fig. 167.—Diagrams of digital tips. *1*, reptile claw; *2*, carnivore claw; *3*, ape; *4*, man; *5*, horse's hoof. *cor*, corneum; *Mal*, Malpighian layer of epidermis; *U*, unguis; *S*, subunguis; *P*, pad. *2a–5a*, ventral views of corresponding long sections shown in *2–5*. (After Bütschli.)

so placed as to converge to a point at the end of the digit. The convex dorsal plate, *unguis*, is rounded in two directions, toward the tip and toward the lateral margins. The smaller central plate, *subunguis*, which is pinched in between the lateral edges

of the unguis, is more flattened and of a less dense texture. Both structures are entirely produced by the Malpighian layer of the epidermis.

2. Claws of Birds

In most cases the claws of birds are confined to the toes, although *Archæopteryx*, the oldest known bird, had three finger-claws on each wing, while some existing types of running birds (*Ratitæ*), have claws on the degenerate first and second fingers. The young hoactzin, *Oposthocomus*, of British Guiana, also has claws on its wings which enable it to venture from its nest and to scramble about in the trees on all fours like a lizard (Fig. 168).

Fig. 168.—Young hoactzin, climbing a tree by means of claws on wings. (After Lucas.)

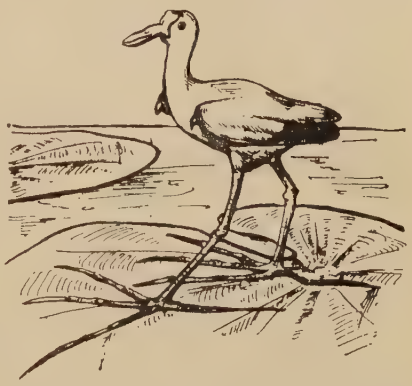


Fig. 169.—Mexican jacana, *Parra*, with long straight claws which increase its ability to run over lily pads without sinking in the water. The male also has spurs on its wings with which to fight. (After Plate.)

In general pattern the claws of a bird are reptilian although they assume a wide variety of forms adapted to correspondingly different functions. Those of a chimney swift, or a woodpecker, for example, are slender and sharp for hanging on to rough surfaces; those of the domestic fowl are blunt and stout for scratching; those of hawks and owls are hooklike talons for grasping prey; while the Mexican jacana (Fig. 169), has long straight claws on the ends of its elongated toes, enabling it in capturing its insect prey, to ski over unstable lily pads that float on the surface of the water.

Certain species of the grouse family (*Tetraonidæ*), undergo a periodic shedding and renewal of the entire claw, reminding one

of the changes undergone by other epidermal structures, such as the antlers of a buck, or the corneal layer of a snake's skin.

3. Claws of Mammals

Mammalian claws cover, somewhat like a thimble, the terminal bony phalanx of each digit. They consist (Fig. 167, 2), of the unguis and subunguis of the reptilian claw, and besides of a terminal *pad*, or cushion, on the ventral side of the digital tip, just behind the claw itself. The animal bears its weight upon these cushions, the corneal layer that clothes them being considerably thickened in consequence. Usually the dominant unguis becomes laterally compressed and curved down to a point, with the result that the subunguis is much reduced. The claws of a cat are sharp and retractile within a protective sheath (Fig. 170), thus being kept unworn to be extended for use only in emergencies. The dog has duller claws, that are more exposed at all times, and particularly so when it runs, for then, they may together with the pads, even come into contact with the ground.

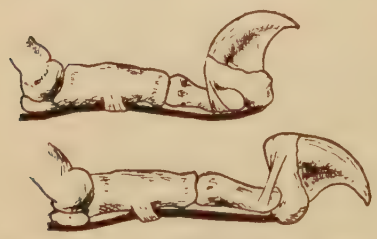


FIG. 170.—Retractile claw of a cat. (After Hesse.)

Bats and sloths have claws developed into elongated hooks which, though making locomotion on the ground awkward and difficult, are very useful when these animals hang themselves upside down, as is their habit.

There are two striking modifications of mammalian claws. In one case the unguis thickens enormously into a shoelike *hoof*, which is so convex that its edges reach all the way around to the ventral side and come into contact with the ground. In the other case the unguis becomes flattened into a conspicuous *nail*, the subunguis shrinks into a narrow rudiment under the projecting eaves of the nail, and the terminal pad becomes transformed into a sensitive ball, occupying the entire ventral side of the digital tip.

4. Hoofs

In a typical hoof (Fig. 167, 5), such as that of a horse, the subunguis fills in ventrally the space between the edges of the unguis, while behind this the pad forms into a tough mass of material,

called the "frog," that serves somewhat the same purpose as a rubber heel on a shoe. Hoofs, like the thick-soled shoes of a traffic policeman, are designed to support the heavy weight of the body in such animals as bear their weight for long periods while standing, and which need a firm foundation. The heavy elephant, which has a hoof on each toe, is particularly well provided with "rubber heels" (Fig. 171).

Fig. 171.—Foot of an elephant showing separate hoof for each toe and a "rubber heel." (After Schmeil.)

The surefootedness of hoofed animals, such as the donkey and mountain goat, is in part due to the fact that the softer subunguis wears away faster than the harder outer edge of the unguis, thus insuring a constantly well-shod foot with a sharp, hard edge, in spite of destructive contact with the rocky ground.

5. Nails

Nails occur in man and other primates where they reinforce and protect the sensitive finger pads, which play such an incalculable rôle in life. When one attempts to pick up a pin, for example, with the fingers encased in gloves, thus lessening the sensitivity of these organs, he is brought to realize how much he depends upon the sense of touch in the finger tips.

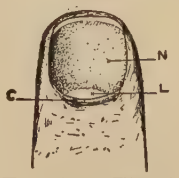


Fig. 172.—Tip of finger. *N*, nail; *L*, lunula; *C*, corneum (*eponychium*) encroaching upon the nail at its base.

The human nail, which corresponds to the ungual part of the claw flattened out, is made up from the closely compacted epidermal cells of the stratum lucidum, or the lifeless remains of what were once Malpighian cells. Whenever transient white flecks appear in finger nails they are due to accidental air-spaces imprisoned between the dead, horny scales of the stratum lucidum. During growth the distal part of the nail is continually advanced toward the tip of the finger or toe by additions from the thickened germinal matrix of Malpighian cells at the base, the position of which, particularly on the thumb, is marked by a white half-moon, or *lunula* (Fig. 172). The pinkish color of the nail, aside from the lunula, is due to its translucency, which allows the blood beneath to show through. The whole nail pushes out through the superficial corneal layer of the epidermis, leaving a ragged

posterior margin of corneum, the *eponychium* (Fig. 173), that may be seen encroaching over the lunula. Under the free outer edge of the nail, where the continuity of the corneum is again broken, is a narrow transitional region which is all that remains of the subunguis of the reptilian claw. Dirt collects here. The refinement of manicuring consists largely in attending to the ragged frame of corneum through which the nail itself projects.

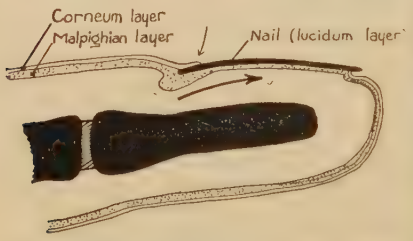


Fig. 173.—A diagram of a long section through a finger tip, showing the relation of the corneum and the Malpighian layer to the nail. The large arrow points the direction of growth, and the small arrow indicates the lunula region, where the Malpighian cells are most active.

Fig. 174.—Chinese finger nails that have been allowed to grow untrimmed. (After Martin.)

The rate of growth of human nails, which may be easily noted whenever one establishes a landmark for reference by accidentally hammering a finger nail and making a "blood blister," is roughly an inch in six months. If never trimmed or broken, nails ought theoretically to be over ten feet long when one reaches the allotted age of threescore years and ten (Fig. 174).

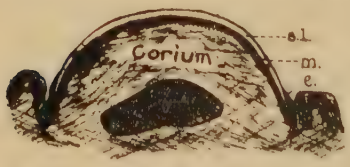


Fig. 175.—Cross section through the finger tip of a child showing relation of epidermal layers in the formation of the nail. *e*, eponychium, the part of the corneal layer that encroaches upon the nail; *m*, Malpighian layer; *s.l*, stratum lucidum which forms the nail. (Bone is shown in black.) (After Lewis.)

In the human fetus the twenty nails appear as terminal amphibian-like epidermal thickenings at about the ninth week. By the twelfth week they are perfectly formed, but it is not until considerably later that they finally migrate into their dorsal position (Fig. 175).

The transition from the laterally compressed claws of most mammals to the flattened nails of primates, is seen in certain lemurs which have claws on some of their digits and rounded nails on others (Fig. 176).

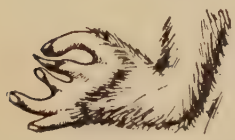


Fig. 176.—Left foot of a lemur, *Perodicticus*, showing four nails and one claw. (After Huxley.)

D. Miscellaneous Corneal Structures

Horny *beaks* are epidermal structures characteristic of birds, the toothless turtles, and monotremes. Among birds, particularly, they exhibit a great diversity of form, and serve a wide range of uses.

Some male birds such as gamecocks, for example, also develop horny *spurs* upon the legs with which they settle questions of supremacy upon the avian field of honor (Fig. 177). The male jacana, which strikes at its rival with outspread wings, is armed with effective wing-spurs (Fig. 169).

Fig. 177.—Spur of a fighting cock.

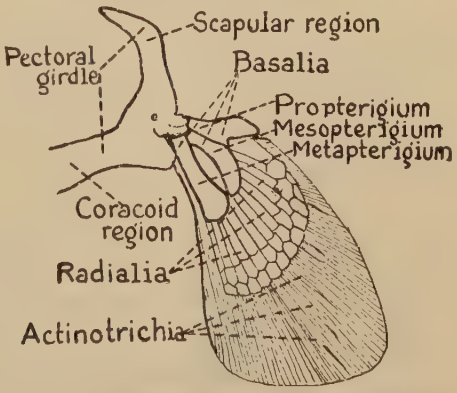


Fig. 178.—Pectoral girdle of a dogfish, showing *actinotrichia*, or horny rays. (After Parker and Haswell.)

Many fishes have horny, epidermal, supporting rays, *actinotrichia* (Fig. 178), as well as bony elements, between the folds of skin that constitute the fins.

The great sheets of "whalebone" (Fig. 179), with their frazzled edges (Fig. 180), that fill the mouth cavity of toothless whales with an elaborate mechanism for straining the myriads of small marine organisms upon which these giants feed, are not "bone" at all, but horny epidermal structures that have assumed a position inside the mouth.

The *rattle* on the tail of a rattlesnake (Fig. 181) is a unique corneal apparatus. Each time, as the snake molts the outer layer of the epidermis, a button or ring of corneum remains behind to record the fact. These rings are dry and loose enough to make a rattling noise when the thrill that an excited snake feels reaches the tip of the tail.

Camels and dromedaries are provided with thick corneal *knee pads* (Fig. 182), which protect these heavy "ships of the desert" when they collapse to a kneeling posture before lying down upon the sands, while the astonishing crimson and lilac *callosities* upon the seat of the African mandrill, are still another kind of epidermal modification, serving these interesting baboons as peripatetic sofa cushions.

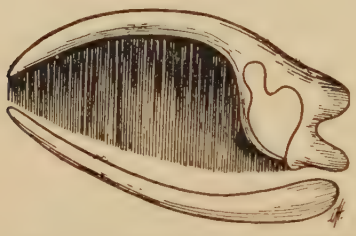


Fig. 179.—Jaws of a whale, *Balæna*, with plates of "whalebone" hanging from upper jaw. (After Nuhn.)

Fig. 180.—The lower end of a single "whalebone" plate, showing the horny brushlike edge that serves as a retaining strainer for the microscopic animals taken into the mouth. (After Nuhn.)

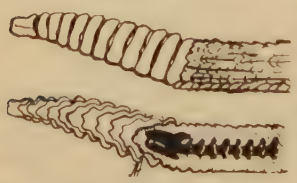


Fig. 181.—The rattle of a rattlesnake, *Crotalus*, with eleven rattles. The lower figure is a long section, showing the vertebræ in black, with the horny rattles fitting loosely one over the other. (After Garman.)

Fig. 182.—Knee pad of thickened corneal substance on a camel. (After Jansen.)

3. Feathers

Feathers are integumentary structures characteristic of birds. They are extraordinary modifications of the epidermis,—strong, light, elastic, and waterproof,—which are particularly fitted to the needs of animated flying machines. In the Jurassic Period, when birds made their debut, so far as is known with ancient *Arch-*

æopteryx (Fig. 44), they were clothed with unmistakable feathers, probably homologous with reptilian scales, although evidence for this is mostly embryological, since neither comparative anatomy nor palæontology show any transitional structures between scales and feathers. The apparent scales on the wings of the sea-going Antarctic penguins are not scales at all, but miniature flattened feathers, as a close examination at once reveals.

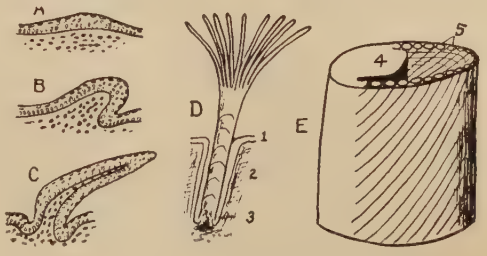


Fig. 183.—Developing feather. *1*, epidermis; *2*, corium; *3*, papilla; *4*, shaft; *5*, barbs. The rolled-up embryonic feather, *E*, splits down the side opposite the shaft and flattens out. (After Hesse.)

The germ of a *developing feather* appears as a hollow papilla of epidermal cells which sinks somewhat into a pocket of the skin (Fig. 183). The epidermal papilla is filled at first with a plug of dermal cells from below, but as the epidermis becomes hard and cornified, this dermal plug withdraws, leaving the hollow lifeless quill inserted in the skin (Fig. 184). The embryonic feather is thus at first

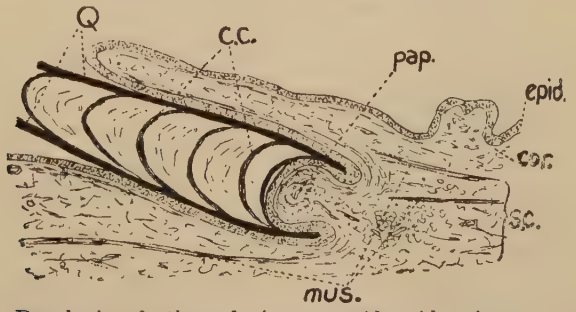


Fig. 184.—Developing feather of pigeon. *epid*, epidermis; *cor*, corium; *s.c*, subcutaneous layer; *pap*, papilla; *Q*, quill; *mus*, involuntary muscle; *c.c*, corneal cups left in the quill by the withdrawal of the papilla. (After Krause.)

a tube of cornified epidermis, set in a pit of the corium. Inside the tubular embryonic feather the wall down one side is thickened, and later becomes the shaft from which the slanting barbs of the developed feather extend. That portion of the tube opposite the shaft, which is the region of the distal tips of

the future barbs, is very thin, and along this thin line the rolled-up feather splits, before it spreads out flat to assume its definite shape.

A *typical feather* (Fig. 185), therefore, is an elaboration of the lifeless corneal layer of the epidermis. It consists of a horny

Fig. 185.—A typical feather from a pelican. (Drawn by Martha S. Whitmarsh.)

shaft, hollow at the inserted end, from the sides of which the lateral *barbs* and *barbules* extend. The barbules on the sides of each barb, like microscopic crochet hooks, interlock with those of the neighboring barb (Fig. 186), thus forming a continuous expanse, called a *vane*, that makes a fanlike surface resistant to air when in motion.

There are three kinds of feathers, namely, *quill*, *down*, and *pin-feathers*. Quill feathers may be further described as *tail*, *wing*, and *contour feathers*, devoted respectively to the functions of steering, flying, and thatching. Tail and wing quills are larger and more rigid than the lighter and more delicate contour feathers that serve to fill out the inequalities of the surface of the body, giving grace of curving outlines to a living bird, but conspicuously absent in a dead bird from which the feathers have been plucked.

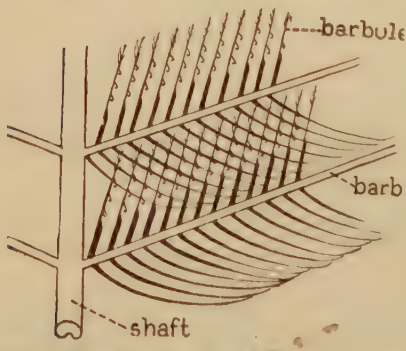


Fig. 186. Detail of a feather. (From Plate, after Mascha.)

There are two kinds of down feathers, namely, *powder down* (Fig. 187), and *nestling down*. Powder down feathers are characteristic of adult birds, and are concealed among the contour feathers, being particularly abundant on the breast and abdomen of herons and birds of prey, where their heat-retaining quality

aids in the incubation of the eggs and the protection of the semi-naked nestlings. Moreover, they shed tiny, powdery scales, together with fragments of delicate, fragile barbs, thus effecting a sort of sanitary cleaning of the plumage in those birds whose nests are particularly liable to be daubed with excreta and the remains of animal food.

Pinfeathers, which superficially resemble hairs, are complemental in structure to down feathers, since they have practically no barbs, but instead consist almost entirely of the shaft, which is missing in down feathers. Pinfeathers are scattered quite generally over the body among the contour feathers, although in certain birds, such as flycatchers and whippoorwills, they become localized about the mouth opening, where, like a *chevaux de frise*, they aid in entangling insects caught on the wing.

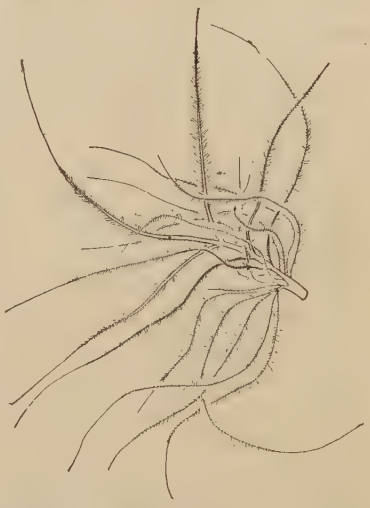


FIG. 187.—A powder down feather. (Drawn by Martha S. Whitmarsh.)

In a quill feather, stabilized interlocking of the barbules occurs only in that part of the vane which is not covered by other feathers, while the shaft does not project outwardly, but is smooth and flush with the exposed surface, thus minimizing frictional resistance during passage through the air. Upon the effective downstroke of the wing, the vanes of neighboring feathers close up together, presenting to the air a common impervious surface, and upon the return upstroke separate somewhat, letting the air through with less resistance. An entirely different arrangement is characteristic of down feathers which have nothing to do with locomotion, since they are merely tufts of free barbs, the barbules of which are without the dominant shaft of the quill feather.

The *plumage* of a bird consists of all the feathers taken together. It is periodically shed and renewed. The *first plumage* of young birds is the transient nestling down, which appears as fluffy tufts on the tips of the emerging contour feathers. In due time these nestling feathers wear off and are replaced by the unfolding

quill feathers. In the first plumage it is the tip of the epidermal tube that frays out like a brush to form the nestling down feather, which is fated to wear off after temporary service. The nestling down is replaced by the *juvenal plumage*, which is made up of the first coat of true quill feathers. This lasts the young bird through its first winter, when in most cases it is replaced by the *nuptial plumage* that heralds the first love affair in the spring. In autumn, after the adventure of raising the first family has been accomplished, the nuptial plumage, now faded and shabby, is exchanged for a *postnuptial plumage*. Every year thereafter that the bird lives, there is a new postnuptial plumage after the breeding season and, in the case of many birds, an additional nuptial plumage in the spring.

This process of exchanging one coat of feathers for another is called *molting*. When a dead feather loosens from its socket in the skin and is lost in molting, the living Malpighian epidermal cells at the bottom of the pit in the skin, backed up by nutritive resources from the underlying corium, grow out into a new embryonic feather tube, which in turn unrolls to take the place of the one that was lost. Water birds, gallinaceous birds, and birds of prey are said to be *precocial*, because they hatch out fully clothed in nestling down, while certain other birds, such as kingfishers and woodpeckers, are described as *altricial*, because they hatch almost naked and only subsequently acquire their first dress of feathers.

Although the feather coat forms a remarkably complete covering over the body, the insertion of individual feathers in the skin is by no means equally spaced. Feathers are attached in localized patches, called *pterylæ* (Fig. 188), between which there are naked areas, *apteria*, which are covered by overlapping feathers from neighboring pterylæ. No doubt apteria in such areas as the "armpits" and the inguinal region, facilitate freedom of locomotion in much the same way as do loose running trunks on the legs of a sprinter. Apteria on the abdomen of a bird may also be useful during incubation, because the eggs are thereby snuggled into more direct contact with the warm body of the brooding mother. The constancy and orderly arrangement of the various pterylæ has been used by systematists in determining the relationship of different kinds of birds for purposes of classification. Ostriches, toucans, and modern penguins are apparently exceptional, in

that they do not, in adult life, show the arrangement of feathers in pterylæ and apteria, but that this is merely a secondary and not a primary condition is indicated by the fact that fossil (Tertiary) penguins, and embryonic ostriches, show distinct pterylæ.

Local deviations in feather arrangements, usually associated with secondary sexual characteristics, are frequent, as, for instance, the crests and ruffs of various birds, and the spectacular tails of peacocks and fantail pigeons. In that strain of fancy poultry known as "frizzles," the plumage has departed from nature's

FIG. 188.—*Pterylæ*, or feather tracts on the body of a cock. (After Nitsche.)

approved style by reason of the twisting of the feather shafts, but it is doubtful whether these curious frowzy birds could successfully maintain themselves out of domestication.

The shingle-like *lay of the feathers* is, with reference to the bird's locomotion, directed from the head toward the tail. This makes possible the retention under the feathers of a layer of warmed air next the skin during rapid flight, which would be blown away if the feathers were arranged in any other fashion.

The remarkably varied *color* of feathers is due to one or both of two factors, namely, chemical pigments and the physical refraction of light. The latter cause gives rise to iridescent effects, like that seen on the throat of a male hummingbird, whereby changes of color result from changes in the angle of observation. The usual pigments are black, red, and yellow, other colors being combinations of these fundamental ones. Pigments are deposited mostly

in the exposed parts of feathers, and only during the period of their growth. After they have become differentiated lifeless structures, there is no way to add pigment granules to them, so that change in color of plumage can then only occur by the fading of pigment in the feathers, by the wearing away of parti-colored tips, or by the complete molting of old feathers and their replacement by new ones. The color of nearly all green feathers is due to refraction instead of pigmentation, although a green copper pigment has been extracted from the feathers of the West African "touracou," *Turacus*.

Frequently contour feathers present complicated variegations of colors which combine to form *patterns*, involving parts of many neighboring feathers. Thus a white wing bar or a blotch on the breast, is in reality a baffling mosaic, made up of unequal fragmentary contributions of color from many separate overlapping feathers, which have grown independently into harmonious positions with reference to each other. No wonder that Darwin is said to have remarked that trying to think out a peacock's tail feather made him actually sick!

In the process of molting, the feathers in the middle of the separate pterylæ are the first to fall out, and this loss and its replacement extends from these centers to the margins of the different feather islands. Sometimes a molt is incomplete and does not involve each entire feather, but is simply the wearing away of a colored tip. This may be quite effective, however, in accomplishing a change in general appearance, as, for example, in the case of the male bobolink (*Dolichonyx oryzivorus*), which, by the gradual wearing off of the differently colored feather tips, changes from a distinctive coat of black and buff patches in the spring to an inconspicuous, streaked, sparrow-like plumage in the fall.

4. Hair

Just as feathers characterize birds, so hairs are the integumental hallmark of mammals. Even such apparently hairless mammals as whales and sea cows, are clothed before birth with embryonic hair, while the bare, thick-skinned rhinoceros and hippopotamus have sparse, bristly hairs about the snout, and the big, naked elephant has a small tuft of hair at the end of its ridiculous tail.

Hair serves a variety of uses besides the obvious benefit of affording general protection. The air-imprisoning pelt of a fur-bearing animal retains the body temperature; the thick mane of a wild horse is a specially placed buffer against carnivorous enemies, pouncing upon its otherwise unprotected neck; the squirrel's frisky tail is a portable blanket in which it can conveniently enwrap itself; the long hairs of a horse's tail form an effective brush to ward off pestering insects; the stiff sinus hairs, or *vibrissæ*, that supply the snouts of many mammals, are sensitive "feelers" (Fig. 189); and lastly, whatever color scheme is carried out upon the body of mammals in general, is due principally to the hairs as color bearers.

FIG. 189.—Vibrissæ of a cat. They form a sensory halo that determines a hole large enough for the body of the cat to pass through.

In structure a single hair (Fig. 190) is an epidermal *shaft*, projecting usually at an acute angle from a pit or depression in the skin. That part of the hair concealed in the pit is the *root*, which expands at the base into a club-shaped *bulb*, where living Malpighian cells that continuously produce the dead shaft from below, are concentrated. Directly beneath the bulb, and in intimate contact with it, is an upward-projecting *dermal papilla*, containing capillaries and nerve endings which supply the hair root. Two corneal layers of cells, namely, *Huxley's layer* on the inside and *Henle's layer* on the outside, surround the root, and together constitute the *inner root sheath*. Other epidermal cells that form the *outer root sheath*, line the walls of the pit. The root of the hair with its two sheaths makes up the *hair follicle*. Opening into the pit from the side are *sebaceous glands*, which produce an oily secretion that renders the dead hair shaft less dry and brittle.

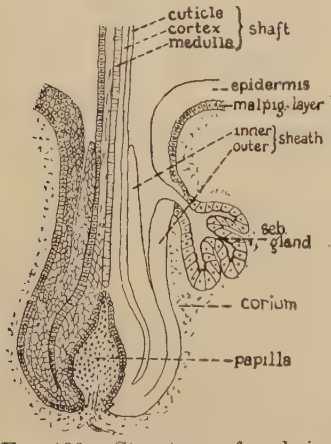


FIG. 190.—Structure of a hair. (After Haller.)

In cross section a hair shaft (Fig. 191), typically shows three kinds of cells, namely, an inside core called the *medulla;* a sur-

rounding ring, the *cortex*, making up the bulk of the hair; and a thin, outer, single layer of shingling cells, the *cuticle*.

Although the root of the hair may be embedded deep in the corium, the entire structure is epidermal in origin, except the papilla which is dermal. The shaft of the hair usually tapers towards the free end and does not branch, although bristles sometimes split distally. Frequently hairs taper also toward the root end, particularly near the point where they emerge from the skin, so that they tend to bend easily, or give way, instead of breaking off upon rough contact with external objects.

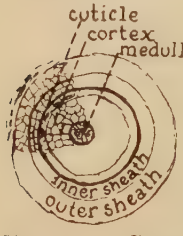
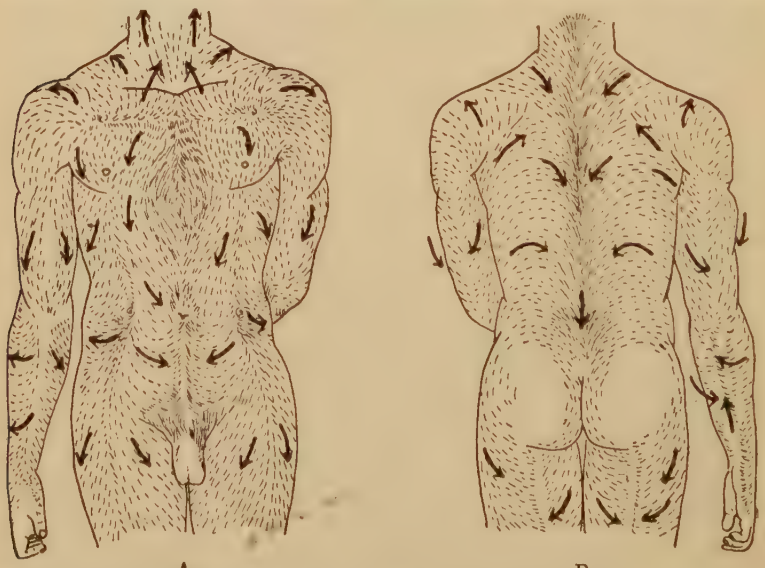


FIG. 191. — Cross section of hair.

Each hair is supplied with a strand of involuntary muscle, *arrector pili*, running from near its base to the superficial region of the corium, on the side toward which the hair slants. When this muscle shortens, the



A B

FIG. 192.—Diagram showing, *A*, the more usual hair currents upon the front or ventral aspect of the trunk, and, *B*, on the back or dorsal aspect of the trunk. (After Kidd.)

hair tends to "stand on end," and, if this condition is pronounced, the skin assumes the appearance of "gooseflesh." The action of the *arrectores pilorum* is particularly noticeable upon the

scruff of an angry dog's neck, or upon the tail of a frightened cat, when these animals take on a more terrifying aspect as the result of this reflex.

The slant at which single hairs emerge from the skin varies in such a way that, in their direction, the hairs, taken together, form vortices and streams as they lie over the surface of the body (Fig. 192). This is particularly apparent in the horse or short-haired dog. *Convergent vortices* form around the base of projecting structures, such as horns, the tail, and the umbilical cord. These hair whirlpools persist even after the structure around which they converge has disappeared. For example, in man they persist about the umbilicus, and at the spot in the coccygeal region where the vanished embryonic tail was formerly located. Perhaps the most familiar example of *divergent whirlpools* is on the human scalp at the vertex of the crown, where the hairs are centrifugally arranged. Other divergent vortices appear in the axillæ and around the nipples, the latter being particularly apparent in men with hairy breasts. The coarse hair of the sloth is divergently parted down the mid line of the belly, instead of down the back as in most animals. This is an adaptation for shedding the rain, since these animals customarily hang suspended upside down from horizontal branches of trees.

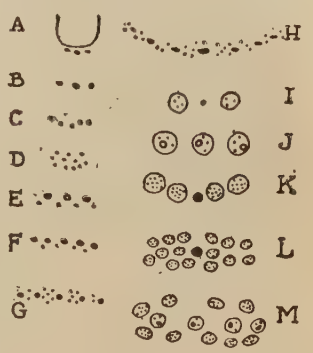


Fig. 193.—Hair groups of different mammals. *A*, *Myoptamus*, a 3-group behind a tail scale; *B*, *Midas rosalia*, 3-group of back; *C*, *Cercopithecus cephus*; *D*, *Ericulus nigrescens*; *E*, *Cœlogenys paca*; *F*, *Tragulus javonicus*; *G*, *Dasyprocta aguti*; *H*, *Loncheres cristata*; *I*, *Auchenia paca*; *J*, *Canis familiaris*; *K*, *Ornithorhynchus*; *L*, *Castor canadensis*; *M*, *Lutra vulgaris*. (After de Meijere.)

Although hairs are not arranged in definite patches like the pterylæ of feathers, yet they do emerge from the skin embryologically in orderly array with reference to each other (Fig. 193). In man they appear in groups of twos, threes and fours, with the largest hairs in the middle of each row (Fig. 194). These rows in turn are spaced in such a way as to suggest that each group is homologous with a scale. This idea is further borne out by the arrangement of the hair groups in other mammals, particularly those of the armadillo and the anteater, where scales are

actually present with a definite group of hairs behind each scale (Fig. 195).

In mammals other than man, localized masses of hair appear as fetlocks, tufts, manes, and as tail modifications of various sorts. It is because of the peculiar arrangement of hairs on the tail that a horse brushes away annoying flies with a "swish" of long hairs, while a cow accomplishes the same result with a "flip" of a terminal tassel.

Fig. 194.—Tangential section through the human scalp, showing the grouping of hairs. (Enlarged 60 times.) (After Martin.)

Hairs occur in various shapes and forms all the way from hard rigid *spines*, like those of the porcupine, hedgehog, spiny mouse, and Australian anteater, to the soft delicate *wool* of sheep and goats. The *bristles* of swine are stiff, elastic hairs, with split ends, in which the outer cuticle layer predominates. *Fur* is composed of dense, soft hairs, frequently lacking the medulla, with a few long coarser hairs interspersed. *Wool* is usually rough or scaly on the surface, and twisted. Consequently it spins well because the separate hairs interlock easily. *Sinus hairs*, or "feelers" (Fig. 189), that radiate from the inquisitive noses of nocturnal prowlers, such as cats, rats, and weasels, are each seated in a large papilla especially well provided with nerve endings, so that any chance contact which disturbs the stiff outstanding shaft, is communicated at once to headquarters through the mechanical agitation of the sensory papilla.

Fig. 195.—Scales and hairs from the tail of the anteater, *Myrmecophaga*. (After Weber.)

The unusual beard on the faces of goats and man is the very latest evolutionary style in hair differentiation. That the beard is not a relic of the past but a prophecy of the future, is evidenced by its sharp differentiation in the male sex, by its late appearance in the individual, and by the fact that it is much less apparent in the more primitive races.

Although man is the least hairy of the mammals, with the exception of the aberrant whales and sea cows, a comparison of his

embryological development shows his close relationship to the other members of the order of Primates. The first evidence of hairs in the human skin is in the form of bunches of epidermal cells which, because of the displacement resulting from their rapid multiplication, grow down like plugs into the corium (Fig. 196). These epidermal plugs become the hair follicles. The bulb of each follicle, with its surrounding outer and inner root sheaths, soon differentiates, and the newly formed lengthening shaft pushes out towards the surface, loosening the temporary epitrichium which at this time covers the body like a gauzy envelope. The hairs emerge first at about the fifth fetal month, in the region of the forehead and eyebrows, eventually becoming a transient coat of delicate, embryonic fur, called *lanugo* (Fig. 197), which clothes the entire body with the exception of the palms, soles, nails, and the spaces around the apertures of the external genitalia. The lanugo usually reaches its highest development during the eighth fetal month, when it begins to be replaced by the permanent hair, at least over certain parts of the body. It remains longest on the shoulders, and in many instances is still in evidence at birth.

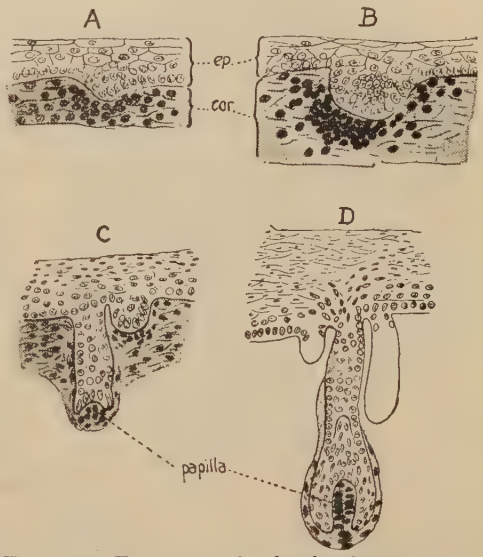


FIG. 196.—Four stages in the development of a hair. *A* and *B* from embryo of sheep. (After Schimkewitsch); *C* and *D* from mole. (After Maurer). *ep*, epidermis; *cor*, corium.

The permanent hair in attaining its growth becomes localized in distribution, and differentiated for various uses. It is thickest on the top of the scalp, since it was originally adapted to shed the rain which fell on our hatless, arboreal ancestors. In apes, which assume a semi-erect posture with the crown projecting somewhat forward instead of upward, the hair is thicker on the scruff of the neck than on the top of the head, as would be expected

from its rain-shedding function. In man hair is also conspicuously specialized in the form of eyebrows, eyelashes, and as guardian of the nasal and external ear passages against dust invasion. At the pubes and axillæ, patches of hair, that perhaps tend to lessen friction, develop at puberty, while the remainder of the human body, which normally appears comparatively bare, is supplied in varying degree with hairy reminders of other days.

Fig. 197.—Face of an embryo five months old with *lanugo*, or temporary hair covering. (After Ecker.)

Hairs are *straight*, *wavy*, *curly*, or *kinky*. In cross section the series varies from nearly round, in the straight head-hair of the Japanese, to elliptical in the kinky hair of the Hottentot (Fig. 121). The papilla of curly or kinky hair is bent or flattened, with the result that the shaft grows out faster on one side than on the other. Pubic and axillary hairs usually curl, even in straight haired people.

According to its manner of growth, hair is either *definitive* or *angora*. Definitive hair grows until a certain length is attained, when the medulla becomes pinched off from its base of supplies in the Malpighian cells of the bulb (Fig. 198). Then the lifeless hair loosens and is shed, and a new hair starts to grow. The interruption in medullary growth at the root of an angora hair, on the contrary, does not occur so often and completely. The shaft continues to lengthen so long as the follicle remains intact. In man the body hairs are definitive, while those of the scalp are angora. This latter circumstance keeps the barbers in business.

The color of hair is due to pigment deposited during growth in the intercellular spaces of the cortex. When hairs "turn gray" there is a reduction in the amount of pigment present, and an increase in the number and size of the light-reflecting air spaces

between the cells. Gray hair in man appears first at the "temples," situated over the temporal bones, which are so called because here the flight of time is marked ("*Tempus fugit*"). In dogs the graying of hair begins on the snout, while in mice and rats it may be anywhere on the body. Some animals, such as the variable hare, *Lepus variabilis* for example, show a seasonal whitening of the hair coat, that brings them into harmony with their snowy habitat in winter, thus insuring them protective coloration.

Data as to particular differences in human hair have been gathered in certain cases. For instance, the head-hair of blondes is usually finer, longer, and more dense than that of brunettes. Some one has made an estimated census, after a partial count, of the number of head-hairs on four females with the following result: blonde, 140,000; brown, 109,000; black, 102,000; red, 88,000. A mathematical moment with a pad of paper and a pencil reveals the fact that, if the typical blonde lady in question should have her hair "bobbed," she might thereby dispose of something like 80 or 90 linear miles of hair.

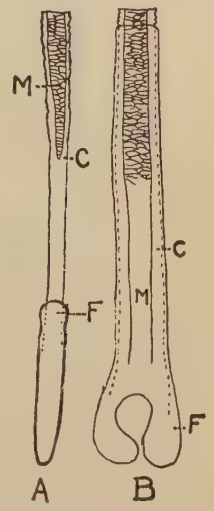


FIG. 198.—*A*, base of hair, fully grown, of definitive growth type. *B*, base of angora hair of indefinitive growth type. (From camera drawings of the same magnification.) *C*, cortex; *F*, follicle; *M*, medulla. (After Castle and Forbes.)

Ecdysis, or molting, which is such a universal phenomenon with other epidermal structures, occurs regularly also in the hair coat. With most mammals shedding the hair is more pronounced in spring and early summer than at other seasons. With man it is a continuous process, involving a normal daily loss which may be increased under pathological conditions. A single head-hair, according to Lewis, lasts for four or five years, while eyelashes are replaced in as many months. A failure in the replacement of the hair of the scalp, results in baldness. There are two general types of baldness. In one the divergent whirlpool of hair about the vertex is the first to go, when the subject comes to resemble a tonsured monk. In the other the hair retreats from the forehead, leaving an increasing expanse of apparent intellectuality with the passing of the years.

Under pathological conditions, unusual abundance of hair (*hypertrichosis*) or abnormal absence of hair (*atrichosis*) may occur. The latter condition is frequently associated with defective development of the teeth. When embryonic lanugo persists it is spoken of as *pseudohypertrichosis* as distinguished from *hypertrichosis vera*, exemplified by the presence of superfluous hair in the case of bearded women and shaggy men.

5. Friction Ridges

Upon the tips of human fingers peculiar ridges may easily be seen, called *friction ridges*, because they aid to a certain extent in preventing the fingers from slipping when brought into contact with objects. Friction ridges should not be confused with the universal tiny furrows and wrinkles that beset the skin. They appear only upon those areas that come habitually into contact with objects, particularly upon the palmar and plantar surfaces of the hands and feet of man, as well as of certain other mammals, and also upon the concave side of the prehensile tail of the long-tailed American monkeys (Fig. 199). They are absent, for example, from the middle of the back, the forehead, and from the rim of the ear, since these regions are not used in taking hold of things.

Fig. 199.—Prehensile tail of a monkey, *Ateles*, showing friction ridges in region of contact. (From Journal of Heredity, April, 1918.)

A histological examination reveals the fact that the epidermis in these friction areas is elevated into ridges on account of a definite development of inequalities in the underlying papillary layer of the corium, and along the ridges thus thrown up pores of sweat glands open, like craters along the peaks of a volcanic mountain chain (Fig. 124). Friction ridges are arranged mostly at right angles to the direction in which there is the greatest tendency to slip, and the sweat glands opening upon them bring about much the same result as when a workman "spits on his hands" before grasping a tool.

The friction areas are intimately associated with padlike epidermal elevations, or *tori*, that originally appear upon the palms and soles. Typically there are eleven of these elevations of the skin

on the contact surface of a hand or foot, namely, five *digital* areas, forming the balls of the fingers or toes; four *interdigital*, on the palm or sole near the base of the digits; one *thenar*, and one *hypothenar*,

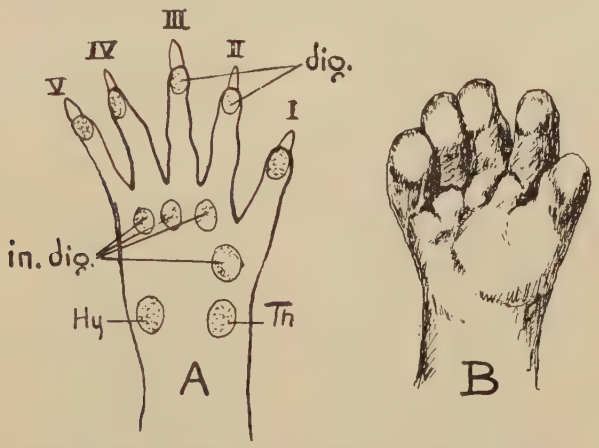


Fig. 200.—Arrangement of the *tori*, or elevations which become the friction areas on the palmar surface of the hand. *A*, diagram of typical arrangement. (After Wilder.) *B*, hand of a human embryo of 22 mm. in which corresponding tori are seen. (After Retzius.) *dig.*, two of the digital tori; *in.dig.*, interdigital tori; *Hy*, hypothenar; *Th*, thenar.

at the posterior part of the palm or sole, on the side of the big digit and the little digit respectively (Fig. 200). Although present as distinct pads throughout life on the feet of certain mammals, the mouse, for example, and also upon the hands and feet of the human embryo, the tori as such disappear in adult man. As

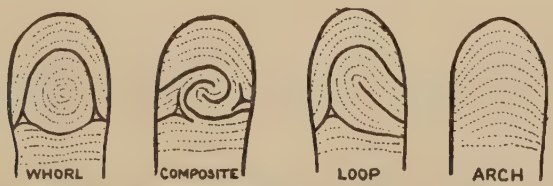


Fig. 201.—Diagrams of the four main types of finger patterns. The whorl and the composite have *two* deltas; the loop, *one*, and the arch, *none*. The loop may be a *radial* loop, or an *ulnar* loop according to whether it opens outward toward the thumb (radial), or toward the little finger (ulnar). (After Wilder and Wentworth.)

the human embryo grows older, these elevations or pads become less pronounced, and eventually are flattened to form the friction areas.

The various minute patterns which the ridges of the friction areas assume, are all definitely established before birth, and retain their individuality, except for slight increase in size, throughout life. Since they are unlike not only in different persons, but also on the twenty fingers and toes of the same person, they furnish an excellent means of personal identification. They may be roughly classified into as few as six general types, namely, *whorls*, *ulnar loops*, *radial loops*, *composites*, *simple arches*, and *tented arches*, as indicated in Fig. 201. The combinations of these

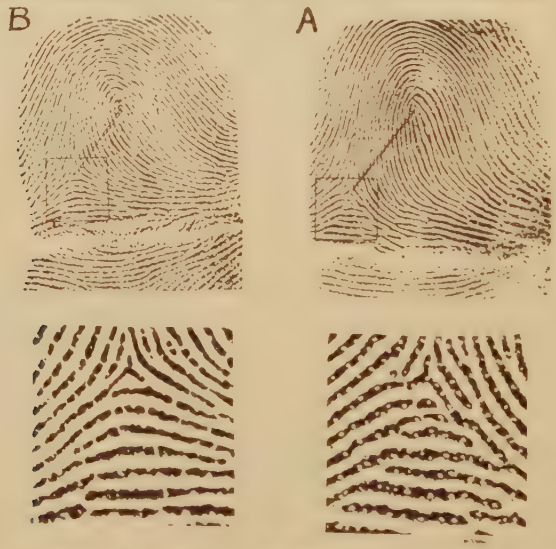


Fig. 202. Two sets of finger prints, superficially alike but quite different in detail. *A*, print of the middle right finger of J. C. (Magnified two diameters.) The area enclosed in the square is shown below in an enlargement of 11 diameters. *B*, print of the right middle finger of J. W. (Magnified two diameters.) This was selected from several hundred prints of middle right fingers in the endeavor to get the nearest match to *A*. The corresponding enlarged square below shows distinct differences that are not evident upon superficial examination. (From Wilder and Wentworth.)

types upon the fingers of both hands taken together, and the infinite variation in the minutiæ that each type reveals upon careful scrutiny, makes possible an almost unlimited subdivision and classification. Thus it has come about that finger-print codes have been worked out, which may even be telegraphed from one part of the world to another in the interests of personal identification.

Just as primitive peoples in the past have frequently employed indelible tattoo marks in order to distinguish themselves unmistakably from their fellows, so friction ridges, which are "nature's tattoo marks," may be made to serve a like purpose. By reason of the fact that finger prints are easily made and kept on file, they can be utilized conveniently in a variety of ways. Upon a bank cheque, passport, or non-transferable document of any kind, for example, such a personal imprint furnishes a unique signature which cannot be forged. In the case of soldiers, sailors, the personnel of large industrial plants, babies at maternity hospitals, inmates of institutions, criminals, undesirable immigrants once rejected, dead bodies recovered from disastrous catastrophies or accidents, aphasia, and in many other instances, finger prints offer a simple and invaluable means of establishing identity (Fig. 202).

Since the time of Galton's pioneer work on finger prints in England,[1] and the appearance of Mark Twain's whimsical classic,[2] in which the imagination of the story-teller anticipated the later applications of science, the serious study and utilization of the ineffaceable friction ridges has developed into a science by itself with a considerable bibliography.

[1] *Finger Prints*, 1892.
[2] *The Tragedy of Pudd'nhead Wilson*, 1894.

CHAPTER XI

INTAKE APPARATUS (DIGESTIVE SYSTEM)

I. IN GENERAL

1. The Whirlpool of Life

Life is manifested as a release of energy that involves continuous death or destruction, for it is only by the breakdown of cells and tissues in which energy has been stored, that life can continue. Thus the paradox that we live by dying. There is, however, more than one kind of death. The kind referred to in this connection is the *local death* of cells and tissues, which is usually accompanied by regeneration and recovery, while what may be called *general death*, that is, death as commonly understood by the term, is that in which the correlation of functions brought about by brain, heart, and lungs, is interrupted so that it cannot again be resumed. Even in this latter case the component tissues may live on for some time after correlation is no longer possible, as shown, for example, by the excitability under electrical stimulation of the muscles of a frog's leg when the frog has been irrevocably killed by the entire removal of its brain and heart.

Huxley has likened an organism to the whirlpool below Niagara Falls. At no two moments of time is it made up of the same mass of water, yet its identity remains, and if photographed on succeeding days from the same point, the pictures would appear alike. All living beings may thus be conceived of as whirlpools of living matter and energy, which nevertheless maintain a continuous individuality, throughout the duration of so-called life. The mechanism that makes good the constant losses that are inevitable in the mortal expense of living, is found in the *digestive system*. It is with the intake aspects of the organic whirlpool that this chapter is concerned.

2. Rate of Living

The rate at which the metabolic waters of life flow through the organic whirlpool varies greatly with the age of the individual.

During the first part of life, while growth is taking place, the intake, like a spring freshet, is greatly in excess of the outgo, but later there follows a prolonged period of balance during which losses of energy are simply made good, until finally the stream of life flows more slowly, and becomes less and less in volume, until it ceases entirely as the head waters gradually dry up.

It is not at all easy to realize the abounding life of animals during the onset of growth. A human baby doubles its weight in 200 days. A newborn mouse quadruples its weight in twenty-four hours, and a silkworm increases its size 500 times during its first day's intake of mulberry leaves. Dr. Keen says:—"Were the same rule to hold, a baby weighing seven pounds at birth would weigh thirty-five hundred pounds the very next day, and when a month old would weigh one hundred and five thousand pounds, or over fifty 'short tons,' which, however, could hardly be called 'short weight.'"

3. Hunger and Thirst

Food, water, and air are the necessary materials taken into a going organism. Food carries energy to be stored in the tissues for later use. Water is the universal solvent necessary for manipulating and shifting about materials within the organism, while air brings oxygen which effects the breakdown of tissues and the liberation of imprisoned energy.

The essential concern of every animal and plant is the securing of these three primary prerequisites for continued activity. This fact is so obvious that one often fails to remember its importance. Anyone who has ever tried to follow the astonishing activities of a single wild bird during the daylight hours of one day, will realize in part the incessant demands of hunger and thirst. Even in the highly specialized routine of human society, the daily program of business, pleasure, education, religion, philanthropy, politics, and all the rest, is secondarily tucked in between meals, and any serious deviation from the periodic exercise of the *sacred rites of intake* are likely to border on the disastrous.

4. The Intake Mechanism of Animals and Plants Contrasted

Most plants are strictly on a diet. The food they use is monotonous in the extreme, yet there is no complaint. It is made up in the synthetic laboratories of green cells, from universally dis-

tributed raw materials, such as carbon dioxide in the air, and water with dissolved salts in the soil, which are taken in through the leaves and roots respectively.

The liquid intake from soil water is soaked up by osmosis through the delicate walls of root hairs (Fig. 203), which quickly collapse upon exposure to dry air. This does not ordinarily happen, however, as the root hairs remain protected in damp soil, since a plant is not forced to travel about to find its necessary liquids.

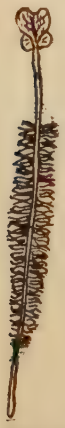


Fig. 203.—Mustard seedling showing root hairs. (After Sachs.)

Animals, however, never have the power of synthesizing foods out of air, water, and inorganic salts, and so they cannot ordinarily remain anchored in one spot, but must forage for food that is already made. Like plants, animals depend upon osmotic intake through thin cell walls (Fig. 204), but these cellular middlemen between the animal body and indispensable food can no longer remain without harm, like the root hairs of plants, on the outside of adventurous locomotor organisms. The intake cells of an animal must be protected from mechanical injury and from drying up while their possessor is seeking food in various places. This is the reason why a *digestive tube* has been evolved in locomotor animals, which is an enclosed passage-way, arranged for one-way traffic, and paved with thin-walled absorbing cells that correspond to the root hairs of plants. Food admitted at the entrance of this protected subway is exposed to the intake cells, which proceed to do their osmotic duty in security, while being transported to fresh fields of food supply. Thus, in one sense an animal may be compared to a plant turned outside-in.

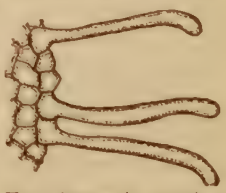


Fig. 204.—A portion of a section through a young root, showing some of the superficial cells growing out of root hairs. A thin layer of cytoplasm (dotted) lines the cell wall and encloses the cell sap. (After Shipley.)

5. The Mission of the Food Tube

While energy is being released in the process of living by the oxidation of the tissues, it becomes imperative that replacements be made from outside sources, in other words, that food must be

obtained. It is not enough, however, to get food, since energy-containing substances cannot be utilized until they are so liquified and transformed that they may be taken into the blood, and thus forwarded to the needy tissues where the actual feeding, or incorporation, occurs. It is the mission of the *digestive tube* to accomplish these transformations. We see the everyday miracle of a cat taking a captured mouse and changing it over into *more cat*, or of human flesh and blood, endowed even with personal idiosyncrasies, made out of the hodge-podge of materials that appear on our bills of fare, and so ordinary are these occurrences that we have ceased to wonder at them.

6. Kinds of Feeders

Animals may be classified according to the prevailing character of their intake, into herbivores, carnivores, omnivores, parasites, symbionts, and saprozoa. *Herbivores* are direct plant feeders. *Carnivores* feed upon animals, but in reality are plant feeders, at least once removed, since the ultimate food of all animals is plants. *Omnivores* feed directly upon both animals and plants. *Parasites* feed upon predigested food at the expense of other organisms which entertain them, without necessarily fatal results to the hosts. *Symbionts*, such as green hydras and green worms of various kinds, probably live vicariously at the expense of microscopic green plants embedded in their bodies, which have the ability to synthesize food on the spot, while *saprozoa* are scavengers, as, for example, flagellates and infusoria, specializing upon dead organisms in the last stages of their reincarnation into inorganic material. Vertebrates belong to the first three groups.

II. THE FOOD TUBE

1. Its Evolution

In the lowest unicellular forms of animal life, the osmotic process of taking in food substances is performed by the outside of the body, somewhat after the fashion of plants, as most simply demonstrated by *Ameba*.

Among sponges, which take the first step in the great adventure of cell association, the method of intake is hardly different, although there is a prophecy of a digestive tube in the ciliated passage-ways that honeycomb the loosely connected sponge mass, through which the food-laden water is made to stream.

That intake is far more important than outgo is evidenced in the entire primitive phylum of the Cœlenterata, by the formation of a mouth opening before any anus is present. Hydras, corals and sea anemones, as well as all other typical cœlenterates, have a *digestive sac* open at one end only, and little else. Everything in these pioneer animals is sacrificed to securing a suitable place for the bestowal of food. The very shape of the body is determined by the food sac, for the animal is simply an animated food bag, decorated around the intake opening with a fringe of subservient tentacles. The importance of the food tube is thus clearly emphasized by its early establishment before that of other structural refinements that mark the animal organism.

Even in echinoderms, of which starfishes and sea urchins are well known forms, although an anus is nominally present, it plays only an occasional rôle, since these devastating, devouring creatures dispose so effectually of the food that enters their maw, that there is little waste left over for disposal at the exit. As a matter of fact in the case of the starfish, most of the food waste is not even taken into the mouth. The stomach is passed out of the mouth in feeding, and the lobes of the stomach encircle the food or prey. Thus the indigestible parts are left behind when the stomach is withdrawn, and there is not much residue to be passed out at the anus.

Worms and caterpillars may well be described as perambulating digestive tubes, with the most important end pointed towards a food-containing world. Directive sense organs cluster around this exploratory end of the food tube, informing it where to go.

Vertebrates are "worms" with additional accessories. Did not the pious Isaac Watts sing in one of his famous hymns, "*What a poor worm am I?*"

A vertebrate is in reality a double tube. The outer tube is the protective body wall, and the inner tube, the digestive canal. Between the two tubes is the body cavity, which makes possible the storage within a limited space of a digestive canal much longer and more efficient than the exterior of the animal would lead one to expect. Thus, the knapsack for carrying the rations is bestowed within instead of being carried outside.

2. Increase of Digestive Surface

So long as the bulk of an animal body remains small, as in the earthworm, a straight digestive tube has enough internal surface

to meet all alimentary demands, but it is mathematically demonstrable that, while the *surfaces* of two homologous solids are to each other as their *squares*, their *masses* are to each other as the *cubes* of their homologous dimensions. This means that the bulk of a growing, or evolving, animal increases more rapidly than its surface, with the result that a straight unmodified digestive tube becomes inadequate to take care of the accompanying mass. This is particularly true in the case of herbivores whose food is less concentrated than that of carnivores, and who consequently need machinery adequate for handling more food in a given time.

There are four general ways in which this need of an increase of digestive surface, which is largely a matter of the intestine, has been met in various animals, namely, by increase in diameter, by increase in length, by internal folds and elevations of various kinds, and by the addition of supplementary diverticula.

A. Increase in Diameter

This method is usually not extensively employed, because of the limitations of space. As the inner tube increases in diameter, the outer tube must also enlarge, which tends to defeat the object to be gained. However, certain regions of nearly every digestive tube, such as the stomach and large intestine, are frequently of greater diameter than the remainder of the tube.

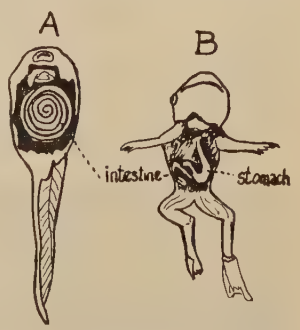


Fig. 205.—Comparison of the tadpole, *A*, and the young frog, *Alytes*, just after metamorphosis, *B*, to show the great difference in the digestive tract with the change from plant to animal diet. (From Bütschli, after Reuter.)

B. Increase in Length

Increase in length is a universal device among vertebrates for adding to the available digestive surface. The body cavity furnishes possible space for stowing away coils and loops of the tube. The characteristic swollen shape of a tadpole, apparently only an animated head with a tail attached, is due to the enormously lengthened digestive tube, which is coiled about many times, packing the body cavity full (Fig. 205). In man the entire digestive tube is between twenty-five and thirty feet in length, although its ends are only about two feet apart.

C. Internal Folds

Increase in diameter and in length of the digestive tube makes demands that soon encounter limits of possible space within the body cavity. Internal folds within the food tube itself, however, avoid this difficulty by adding to the expanse to which the food taken in is exposed.

Fig. 206.—Diagrammatic cross section of an earthworm, showing the typhlosole which increases the internal surface of the digestive tube.

A longitudinal fold extending into the cavity of the tube is termed a *typhlosole* (Fig. 206). Such an arrangement is present in the cyclostomes. In dipnoi, as well as in elasmobranch and ganoid fishes, the intestinal part of the food tube is supplied with a *spiral valve* (Fig. 207), which is simply a typhlosole so much longer than the tube in which it is placed, that it must coil around like a spiral stairway with one margin attached while the other is free.

Fig. 207.—Spiral valve of dogfish. (After Roule).

Certain invading transverse folds, called the *plicæ circulares* (Fig. 208), give a washboard effect to the inner surface of the anterior part of the human intestine, while countless tiny elevations, or *villi*, which project like the nap of velvet from the inner surface of the small intestine, particularly of the higher vertebrates, produce an enormous increase of area in a minimum of space, for contact with passing food.

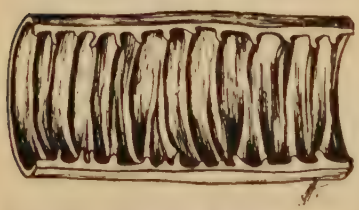


Fig. 208.—Transverse rugæ, *plica circulares*, lining the colon. (After Cunningham.)

D. Supplementary Diverticula

Side alleys, or diverticula, from the main tube occur in many instances. These are particularly abundant in fishes at the junc-

tion of the stomach with the small intestine, where they are called *pyloric cæca* (Fig. 209). They vary in number from one in the ganoid *Polypterus*, and the sand lance, *Ammodytes*, to over 200 in the mackerel, *Scomber*.

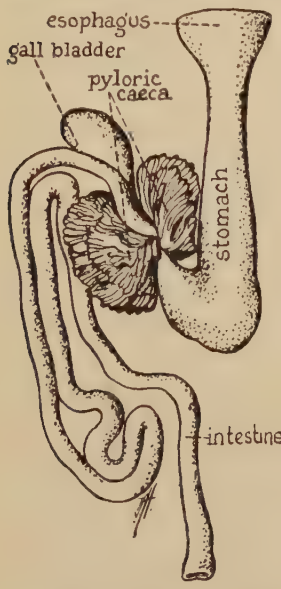


Fig. 209.—Pyloric cæca of a teleost fish, *Merlucius*. (From Schimkewitsch, after Krupski.)

Other diverticula, called *colic cæca*, are found at the junction of the small and large intestines in vertebrates beginning with reptiles. The colic cæcum of a turtle is only a slight enlargement (Fig. 210), but in rabbits and some other rodents it may become an enormously enlarged tube with an internal capacity nearly equal to that of the rest of the digestive canal to which it is attached. In man the colic cæcum, with its troublesome shrivelled prolongation, the *processus vermiformis* or "vermi-

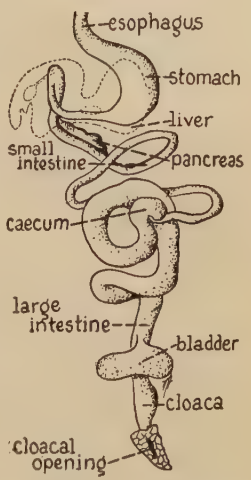


Fig. 210.—Digestive tube of turtle. (The outline of the liver is dotted.) (After Bütschli.)

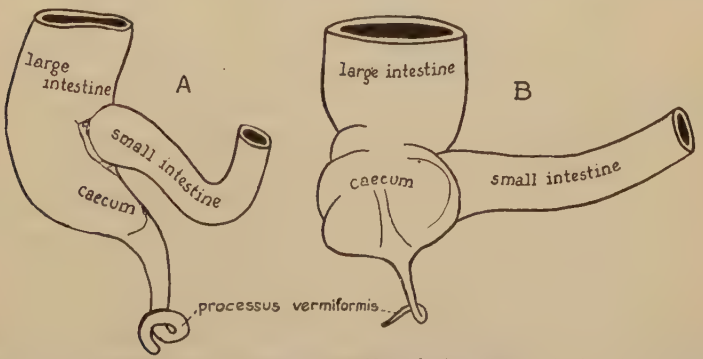


Fig. 211.—Cæcum and processus vermiformis in man. *A*, in the embryo; *B*, in an adult. (After Wiedersheim.)

form appendix" (Fig. 211), has outlived its usefulness and bears an unsavory reputation. Birds typically have two colic cæca (Fig. 212).

The large intestine of man, as well as of several other mammals, is pushed out into a series of baywindow-like enlargements, called *haustra* (Fig. 213), which assume the character of diverticula, and throughout the vertebrate series, there are connected with the rectal region various problematical outpushings, such as the "rectal gland" of elasmobranchs, the "urinary bladder" of amphibians, the "bursa of Fabricius" in birds, and "anal glands" of certain mammals, that have been made to serve several different uses.

FIG. 212.—Two colic cæca of an owl. (After Pycecraft.)

FIG. 213.—Haustra in the large intestine of man, with small diverticula, *glandulæ epiploicæ*. (After Cunningham.)

3. Development

In the earlier stages of a developing amphioxus embryo when the hollow sphere of undifferentiated cells (blastula), pushes in on one side to form a double cup (gastrula), there results a cavity within the inner cup in which food may be held in close contact with absorbing cells. This is the *gastrocœle*, or primitive digestive cavity (Fig. 106, C). The opening (*blastopore*), of this cup soon becomes obliterated by the overgrowth of one side of the blastopore lip with the result that the gastrocœle no longer communicates directly with the outside (Fig. 214). In eggs laden with nutritive yolk, however, it is not at first necessary to receive food from the outside world, since the yolk, stored in the egg itself, has direct access to the newly established gastrocœle, where it is greedily utilized.

The diminishing yolk is rapidly translated into the enlarging embryo, within which the gastrocœle becomes elongated into the

major part of the future digestive canal, lined with entodermal cells, and closed at either end. There comes a time, however, when the increasing demand for nutriment can no longer be supplied from within, and communication with the outside must be established in order to admit food into the tube. This change comes about by the inpushing of the ectoderm until it meets the entodermal wall near either end of the elongated gastrocœle, where it finally breaks through, making a continuous open passage-way.

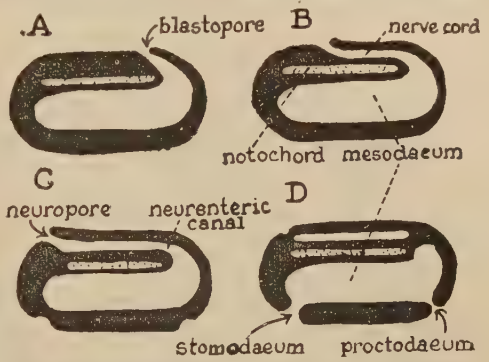


FIG. 214.—Diagrammatic stages in the differentiation of the nerve cord and digestive tube in *Amphioxus*. (After Roule.)

The anterior ectodermal ingrowth is called the *stomodæum*, and the posterior ectodermal part, the *proctodæum* (Fig. 215), while the entodermal region between the stomodæum and the proctodæum, which was originally the gastrocœle, is now termed the *mesodæum*. The embryonic stomodæum stakes out the claim for the future mouth region, and the proctodæum locates the

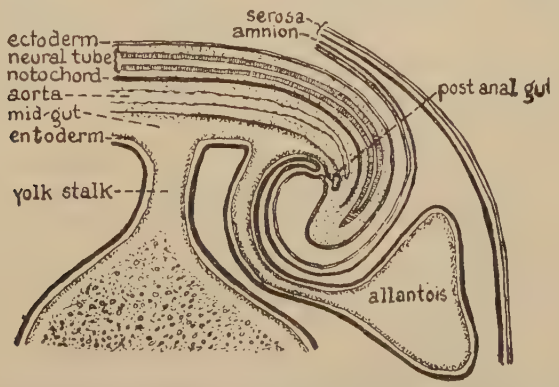


FIG. 215.—Schematic long section of the caudal half of an embryo, to show the formation of the allantois in a chick of about four days incubation. The *proctodæum* is about to break through and leave the postanal gut. (After Patten.)

anus (Fig. 216). The food tube thus consists of three embryonic components, although the landmarks that separate them from each other are obliterated in the adult.

Fig. 216.—Diagram of the formation of the anus in a human embryo, 29 mm. in length. *P*, proctodæum. (After Keibel.)

4. Histology

A cross section of the digestive tube within the body cavity shows it to be made up of several concentric layers of cells (Fig. 217).

The innermost layer, or the *mucosa*, is primarily the original embryonic entoderm, supported by mesodermal connective tissue. The entodermal part is composed of digestive cells which perform the root-hair function of absorption, and from which arise the various digestive glands that bring about the chemical transformation of the food. All other layers are secondary, and are subsequently added to this most important primary lining of the food tube.

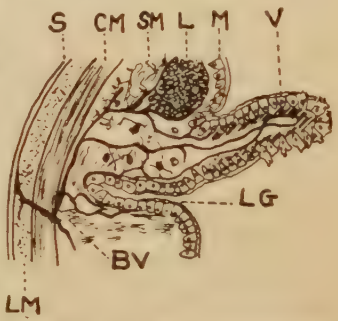


Fig. 217. — Semi-diagrammatic transverse section through the intestine of a vertebrate. *S*, serosa; *LG*, Lieberkühn gland; *V*, villus; *M*, mucosa; *L*, lymph follicle; *LM*, longitudinal muscle; *CM*, circular muscle; *SM*, sub-mucosa; *BV*, blood vessel. (After Wiedersheim.)

Next to the mucosa is the *submucosa*, a layer of connective tissue devoted largely to supporting a rich network of capillaries and lymphatics, that by means of the blood bear away over the body the results of digestion.

Outside the submucosa is a double layer, the *muscularis*, composed of circular muscles on the inside and longitudinal muscles on the outside. These muscles are involuntary in their action, except for a short distance at either end of the tube, where they are under the control of the will. They effect the movement of the food, by the process of peristalsis.

Around the muscular layer on the outside is a sustentative layer of tissue, called the *serosa*, which is continuous, by way of the mesenteries, with the *peritoneum* that lines the body cavity. In that part of the food tube lying outside of the body cavity there is no serosa present, and at the extreme ends, where the

embryonic stomodæum and proctodæum take part, the mucosa is ectodermal rather than entodermal in origin.

5. Regions of the Tube

Since the food undergoes progressive modification as it passes through the tube, the tube itself, as would be expected, will show structural adaptations for the performance of these varied tasks. There has of necessity evolved a physiological division of labor, or a specialization, which has left its mark on the morphological features that characterize the alimentary tract in different regions. For purposes of description the entire tube may be divided into four zones, or regions, namely, ingressive, progressive, degressive, and egressive.

Fig. 218.—Silhouettes of digestive system of fish, amphibian, bird, and mammal. (After Roule.)

The *ingressive zone* is the intake region of prehension and mastication. It involves the lips, and mouth, with the teeth, tongue, and various other structures contained therein. The *progressive zone*, embracing the pharynx, esophagus, and stomach, is the region of conduction and preliminary modification of the food. The *degressive zone*, coincident with the small intestine, is not only the most extensive, but also in a sense the most important part of all the zones, for here occurs the chemical preparation of the food stuffs, and their ultimate selection and absorption into the blood. Finally, the *egressive zone*, which is confined to the large intestine, is the region for the expulsion of the unusable residue, which cannot be diverted into the blood and applied to the uses of the body. These regions, shown diagrammatically in silhouette for fishes, amphibians, birds, and mammals, may be seen in Fig. 218.

We are prepared now to proceed upon an imaginary tour of inspection through the entire alimentary tract, with our eyes open for the anatomical scenery along the way.

III. INGRESSIVE ZONE

1. Food Capture and Prehension

Before food can proceed along the digestive highway, it must be captured and placed inside the entrance of the tube. This process occupies a large part of the waking hours of most animals and even in the case of intellectual man, is the actuating motive of much of his daily behavior.

Probably in the majority of cases, the capture involves some sort of a chase, since both the animal and its food are in motion. Herbivores, however, depend upon food that is generally stationary, so simply need to seek it out. Sedentary feeders remain in one spot, catching motile food which comes their way. Devices of various kinds, therefore, like ciliary whirlpools or stretching tentacles, are employed by sedentary animals to bring food within range, while many animals that are anatomically able to go in pursuit of food, succeed better by lying in wait for passing food than by bestirring themselves in open chase. Such animals frequently develop camouflaging coloration, or, like spiders, construct elaborate snares and traps for their prey.

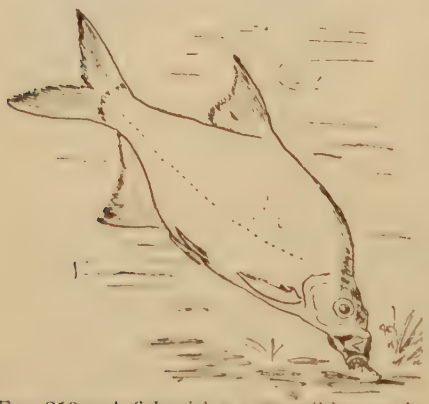


FIG. 219.—A fish with a protrusible mouth, pulling an insect larva out of the muddy bottom. (After Hesse.)

When food is finally within reaching distance, there are many *organs of prehension* (Fig. 219), which are adapted for seizing and placing it within the mouth. These adaptations range all the way from the slow pseudopod of an *Ameba*, to the stretching, reaching arm of modern man. Birds, possessing neither arms nor hands for taking hold of food, have the edge of the mouth opening drawn out into a point, forming a horny

beak which is used as a pair of forceps in picking up things. The prehensile tongue of such diverse animals as toads, anteaters, and cattle becomes a very effective substitute for a grasping hand, while muscular lips, particularly in herbivores, serve a similar purpose in food capture. Many animals, as for example swans and giraffes, have an elongated flexible neck as an accessory organ of prehension, to aid in bringing the mouth into the neighborhood of food. The trunk of an elephant, which is a lengthened nose and upper lip combined, is a unique device for reaching food without the necessity of moving the heavy head.

2. The Mouth Aperture and the Lips

The shape and extent of the mouth opening, which is the Ellis Island of the digestive tract, varies greatly in different vertebrates depending largely upon the different kinds of food utilized.

The limits of the oral slit are set by the fleshy *cheeks*. An animal without cheeks, like an alligator or a nestling bird, can open up its mouth to a surprising extent. Amphioxus and the cyclostomes (Fig. 130), keep the mouth always open of necessity, since structurally it cannot be closed. In man the slit of the mouth normally extends from about the region of the premolar teeth on one side to those on the other side, although there is a considerable range of individual variation, as may be commonly observed.

The puffed cheeks and rosebud mouth of infancy are adaptations for sucking, mammalian characteristics which are largely lost in adult life. The evolution of cheeks in the adult, however, is closely connected with a muscular equipment for mastication, so that it comes about that animals with relatively small mouths are usually better able to chew their food than those with an expansive opening. The refinement of chewing food, with all its train of anatomical consequences, is a mammalian peculiarity, for it will be recalled that fishes, amphibians, birds and reptiles, and even many of the lower mammals, swallow their food without chewing it.

The *lips* are two movable folds at the edge of the mouth aperture. They are covered by skin on the outside and moist mucous membrane on the inside. Between these two regions in man there is an exposed transitional zone, namely, the red part of the lips, which is extremely sensitive to touch because of an abundant supply of nerve endings.

3. Buccal Cavity

Immediately within the mouth aperture is the vestibule, or *buccal cavity*, bounded outwardly by the lips and cheeks, and inwardly by the front face of the teeth and gums. When the mouth is closed and the teeth are in contact, this cavity practically becomes obliterated, but behind the back teeth, and between the closed teeth there is still direct communication with the larger oral cavity within.

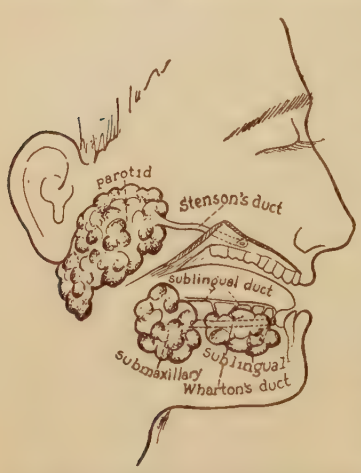


FIG. 220.—Salivary glands and their ducts. (After Cunningham.)

Various glands open inside the buccal cavity. Along the inner surface of the lips are numerous small *labial glands* that secrete mucus. These glands may be easily identified by rubbing the point of the tongue back and forth against the inner surface of the lips, when they will be felt as tiny rough bunches. Other mucus-producing glands, the *molar glands*, penetrate the cheeks and open into the buccal cavity near the back teeth, while opposite the upper middle molar on either side, is the exit of the *parotid* or *Stenson's duct* that drains the large *parotid glands* (Fig. 220) from which saliva flows. It is not difficult to demonstrate the openings of these important ducts, for, if one sticks the tongue into the cheek, and psychologically aids the flow of saliva by looking at a freshly sliced lemon or something that "makes the mouth water," a tiny stream of saliva may be felt spurting into the buccal cavity. Birds, turtles and monotremes have dry cornified buccal cavities nearly devoid of glands.

FIG. 221.—*f*, frenulum under tongue. The openings of Wharton's ducts are at the base of the frenulum on either side. (After Cunningham.)

On the inner face of the upper lip in the mid line, also demonstrable by the exploring tip of the tongue, is a transverse fold of mucous membrane, which tends to hold the lip close against the

gums. This is called the *frenulum*, and a second one occupies a similar position with reference to the lower lip (Fig. 221).

In some animals, such as the Australian duckbill, Old World monkeys (Fig. 222), gophers (Fig. 223), squirrels, and other rodents, the buccal cavity becomes stretchable into distinct *cheek pouches*, which are used for the temporary storage of food when its collection occurs under circumstances of competition such as to make grabbing as much as possible in a minimum time, a necessity. Sometimes greedy little children demonstrate their probable rise from animal ancestry by reverting to the cheek-pouch method of excess disposal of food.

Fig. 222.—Lower jaw of ape, showing, *cp*, lateral cheek pouches; *mm*, masseter muscle; and *mx*, maxilla. (After Nuhn.)

Fig. 223. — Cheek pouches of a gopher. (After Nuhn.)

4. Oral Cavity

Behind the buccal cavity and merging into it, is the *oral cavity*. The *roof* of this cavity in vertebrates generally is the arching palate, which has a skeletal foundation of bone, the *hard palate*, in the front part of it, and is supplemented behind by a flexible addition of connective tissue, the *soft palate*. The hard palate lies within the upper dental arch and is continuous with the *gums*, while the soft palate blends with the lateral walls behind the teeth, presenting a free, hanging, posterior border like a curtain, at the region of the *fauces*, or the gateway leading to the pharynx. The posterior border of the soft palate in man is still further prolonged in the median line into a soft pointed flap called the *uvula*, that projects downward and backward, and which may be easily seen hanging down in the back part of a wide-open mouth (Fig. 224).

Fig. 224.—Open mouth showing uvula hanging down in center, the tonsils (dotted) on either side, and the raphe along the mid line of the roof of the mouth. (After Cunningham.)

Along the median line of the hard palate in man, from a point

near the upper incisors and fading out towards the soft palate, is a faint ridge, the *raphæ*, which indicates that the hard palate is formed by the union of two embryonic components. It may be felt, whenever it is still present in the roof of the mouth, by means of the tip of the tongue.

In many cases there may also be similarly demonstrated a series of transverse folds or ridges, the *palatine rugæ*, diminishing in size from the region of the teeth backward. The rugæ are more in evidence in human embryos than in adults, although they sometimes persist throughout life. They are washboard-like in character and reach their highest development in such carnivores as cats and dogs (Fig. 225), where, no doubt, they aid in securing a surer grip upon any struggling victim that has been seized in the jaws.

Fig. 225.—Palatine ridges in the roof of a dog's mouth. (After Wiedersheim.)

The surface of the entire palate, particularly of the soft palate and the uvula, is beset with numerous *palatine glands*, whose secretion of mucus helps to keep the mouth cavity moist.

The *sides* of the oral cavity posterior to the back teeth, blend with the buccal cavity into a common space, while the *floor* is largely occupied by the bulky tongue, which fills practically the entire cavity when the mouth is closed.

When the mouth is opened wide, and the tongue is raised and curled back, the *frenulum linguæ* (Fig. 221), may be seen, which is a fold of connective tissue along the mid-ventral region that tends to hold the tongue down to the floor of the oral cavity. Occasionally, when the frenulum linguæ is overdeveloped in a human infant, such an individual is said to be "tongue-tied," and a slight surgical operation is necessary before the tongue can acquire the freedom of movement essential for clear articulation in speech.

Extending on either side of the frenulum linguæ in man, and parallel to the teeth, is a crescentic fold of tissue, called the *sublingual ridge*. Along this ridge open the several *ducts of Rivinus* from the sublingual salivary glands, while at the widest part of the frenulum linguæ near the lower incisor teeth, are the two openings of *Wharton's ducts*, one on either side, that drain the

submaxillary glands. Thus, three sets of salivary glands, the *parotid*, *sublingual*, and *submaxillary*, pour their digestive and lubricating secretions of saliva into the buccal and oral cavities of mammals.

This differentiation of mouth glands into the various mucous and salivary glands found in mammals, does not appear among the lower vertebrates. Fishes, which bolt their food without chewing, do not have digestive salivary glands, while mucous glands, the mission of which is to moisten food in the oral cavity preparatory to swallowing, are also unnecessary and practically absent.

Among amphibians, which are on the border-line between submergence in water and life in the air, scattered mucous glands, termed *intermaxillary glands* from their generalized location, make their appearance in some instances, and the protrusible tongue, particularly in frogs and toads, is supplied with *lingual glands*, secreting a viscous mucus that aids in the capture of insects and other moving prey.

In reptiles the mouth glands are more grouped and localized, so that it is now possible to speak of palatine, lingual, sublingual, and labial glands according to their position. All these glands produce fluid to moisten the food, and to render the act of swallowing easier, although it is doubtful if they aid in digestion.

FIG. 226.—Poison gland of snake. (After Kingsley.)

The *poison glands* in the mouth of certain snakes (Fig. 226), are transformed labial glands, while those of the only known poisonous lizard, the "Gila monster," *Heloderma*, of southwestern United States, are modified sublingual glands. Birds, as noted, have a paucity of oral glands. No one ever saw a bird "spit" or "drool," because the mouth is comparatively dry. In the case of mammals, which usually chew their food to some extent, mouth glands of two general sorts are universally developed, mucous and salivary, for the double purpose of lubrication, or liquefaction and chemical modification. Mucous glands are especially essential for herbivores which consume large quantities of comparatively dry, bulky food. The action of the salivary glands, which is chemical as well as mechanical, will be considered later in a paragraph about the digestive glands in general.

5. Tongue

What passes under the name of "tongue" in the vertebrate series, is not always strictly comparable to the "unruly member" in man (or woman), which must be regarded as the outcome of a long sequence of adaptations.

Amphioxus has no tongue at all, and the muscular, piston-like tongue of cyclostomes is such an aberrant, highly specialized structure that it gives no clue to the true beginnings of this organ among vertebrates.

In fishes, however, a *primary tongue* makes its definite appearance. It is a non-muscular elevation from the floor of the mouth cavity, consisting of a covering of mucous membrane, stretched over a skeletal support of cartilage or bone, derived from the framework of the gills (Fig. 227). Whatever movement this type of tongue possesses is due to extrinsic muscles that act upon the skeletal support, in such a way as to enable it to change position but not shape, rather than upon intrinsic muscles that modify both shape and position. It is also not protrusible, although motile enough to aid somewhat in forcing back a mouthful of food to be swallowed, as in the case of certain teleosts possessing prehensile teeth.

FIG. 227.—Diagrammatic lateral view of the skull of a dogfish, showing the splanchnocranium in black. The projecting basihyal cartilage, the most ventral part of the second arch in the diagram, lies between the lower jaws of the first arch, and is the skeletal basis of the fish's tongue. (After Jammes.)

The lower Amphibia, such as the perennibranchiate urodeles, have fishlike tongues of mucous membrane with bony support. In the higher salamanders the horseshoe-shaped groove between the primitive tongue and the lower jaw, becomes elevated, particularly in front, into a *glandular field* (Fig. 228), in which a glutinous mucus, useful in entangling captured insects, is secreted. This glandular field as it gradually rises and thus obliterates the original groove around the under edge of the primary tongue, finally becomes incorporated with the latter as an anterior projection, forming the so-called *secondary tongue*.

In the median line at the junction of the primary and secondary tongues, and originally connecting with the thyreoid gland, there is a tubular downgrowth, the *ductus thyreoglossus*, that persists in mammals as the *foramen cæcum*, to be mentioned again later.

The secondary tongue soon becomes invaded by intrinsic muscles, which greatly increase the range of its movements, and make changes in its shape possible. Of these muscles, the *genioglossals* act as protractors, and the *hyoglossals*, as retractors. In the American salamander, *Eurycea*, they become so efficient that the sticky tongue may be shot out in the capture of insect prey, and retrieved for a considerable distance with incredible speed.

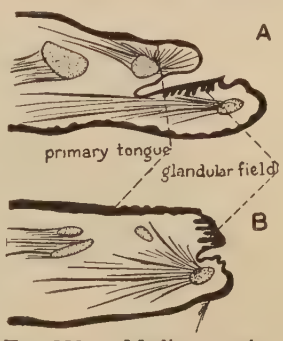


Fig. 228. — Median section through the floor of the mouth, showing the formation of the glandular tongue. *A*, *Triton alpestris*; *B*, *Salamandra maculosa*. In the latter the glandular field is encroaching upon the primary tongue to form the secondary tongue. (After Haller.)

The secondary tongue of most frogs and toads is attached far forward on the floor of the mouth cavity, and at rest is retroflexed so that its point lies backward down the throat. When it is flipped out after an insect (Fig. 229) or a slug, it is "swallowed" upon its return, along with the captured food, and thus restored to its original position. One family of South American toads is named the *Aglossidæ* because, in those exceptional animals, the tongue is either absent or poorly developed.

The reptiles possess a double tongue embryologically like that evolved by the amphibians, but with considerable modification. In turtles and alligators, it is thick and only slightly protrusible, whereas in snakes and lizards it may become extremely extensible. The little wall lizards, or "geckos," for example, can easily lick off the outside of their transparent eyelids with their tongues, while snakes can protrude their delicate, sensitive, forked tongues for some distance through a median notch in the edge of the lower jaw, without "opening the mouth." The chameleon, an arboreal African lizard famous for its kaleidoscopic color changes.

Fig. 229.—Tongue of a frog catching a fly.

at the same time that it grasps the twig of a tree, uses its tongue like a lasso in entangling its illusive prey, in much the same way as the salamander, *Eurycea*, shoots out its tongue from a position on the ground (Fig. 39). The mechanism in the two cases is somewhat different. In *Chameleon* the bony framework of the primary component at the base of the tongue acts as extensible levers to supplement the muscular secondary component of the tongue in its protrusion, which is not the case with *Eurycea*.

FIG. 230.—Tongue apparatus of a bird. *b*, branchial arch to which the extrinsic muscles are attached; *h*, hyoid arch corresponding to the primary tongue; *t*, secondary tongue superimposed upon the primary tongue. (After Lucas.)

In birds the bony framework of the primary tongue, which supports the secondary tongue, is especially developed, since movement, in the absence or reduction of intrinsic muscles in the secondary tongue, is largely through extrinsic muscles attached to these bones. This framework consists typically of a median bone or bones, the *copula* (Fig. 230), and two pairs of lateral bones, the *hyoids*, and *first branchials*, which are relics of ancestral gill arches. A woodpecker, whose horny, spearlike tongue can be projected out of its long beak when impaling a grub, possesses an elaborate skeletal hyoid apparatus, attached at the base of the tongue, which, when at rest is stowed away in coils on either side of the skull underneath the skin. As the tongue is extended, these supporting hyoid coils are straightened out through the action of muscles, while the withdrawal of the tongue to its original position within the beak is facilitated by the elasticity of the hyoids, which snap back into place like released watchsprings that have been temporarily straightened out.

The mammalian tongue, like that of reptiles, is made up of a posterior part corresponding to the primary tongue of fishes, and an anterior secondary tongue, to which lateral components are added.

In a human embryo about four weeks of age, the secondary tongue first appears as an elevation from the floor of the mouth

cavity just anterior to the landmark of the ductus thyreoglossus. This elevation is homologous with the "glandular field" of the Amphibia, and is called the *tuberculum impar* (Fig. 231). On either side of it are lateral swellings from the inner surfaces of the

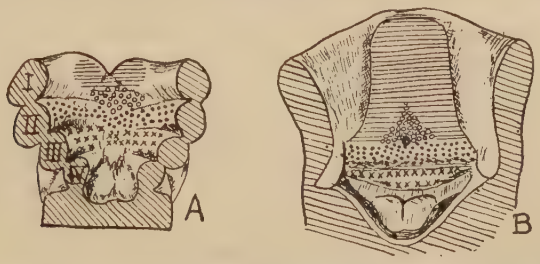


FIG. 231.—Stages in the development of the human tongue. *A*, 6 mm. embryo; *B*, 15 mm. embryo. Contributions from the first three branchial arches (I, II, III) are indicated respectively by parallel lines, dots, and crosses; the *tuberculum impar* is marked by circles. (After Arey.)

two sides of the skeletal mandibular arch, which meet at this point. These swellings soon increase and completely surround the tuberculum impar, eventually forming the bulk of the anterior part of the tongue. In somewhat similar fashion the region enveloping the copula, that is, the skeletal part that forms the foundation of the primary tongue lying behind the ductus thyreoglossus, is augmented by additions from the neighboring hyoid and first branchial arches, to form the "root" of the tongue, or the part of it lying in the pharyngeal cavity (Fig. 232).

FIG. 232.—Floor of the mouth and pharynx of a 7.5 mm. embryo, from a reconstruction. *C*, copula; *F*, furcula; *T*, tuberculum impar; *XX*, the swellings on either side that give rise to the body of the tongue; *I-III*, branchial arches. (After McMurrich.)

The tongue of mammals is highly muscular and consequently capable of a great variety of movements, serving many purposes. It keeps the food between the teeth in the process of chewing, and starts it on its way when ready to be swallowed. It is decidedly prehensile in many herbivores, as cows, for example, who can grasp with it a tuft of grass to be sickled off against the lower incisors. It is a universal toothbrush, giving point to the phrase "as clean as a hound's tooth," and it also serves as a curry-comb for fur bearers, while animals like cats that lap up liquids, use it as a spoon.

Finally, its dorsal surface is thickly beset with sense organs of touch and taste, which stand in readiness to receive the password of admittance from entering food.

6. Teeth

Teeth are primarily devoted to the manipulation of food, either grasping, cutting, or grinding it, although in some instances they secondarily assume other functions, such as defense.

The extreme variability of teeth, adapting them for diverse kinds of work, affords the comparative anatomist much insight into the manner of life of the different animals possessing them, while to the palæontologist they are veritable hieroglyphics which go a long way in aiding him to reconstruct the story of the past.

Fig. 233. — Diagrammatic long section through a typical canine tooth. *E*, enamel; *D*, dentine; *G*, gums; *P*, pulp cavity in which are capillaries and nerve endings; *J*, jaw bone; *C*, cement. (Drawn by L. K. Burdon.)

Teeth are the first hard structures of the body to appear during development, even before any part of the bony skeleton, and although they eventually come into intimate secondary relation with the skeleton, they are in reality derivatives of the stomodæal region of the alimentary tract, and thus morphologically as well as physiologically they are a part of the digestive system.

A. Structure

In structure a typical human tooth (Fig. 233), consists of a *crown*, which projects beyond the gums; the *roots*, which are embedded in the sockets of the jaw; and the *neck*, which is the transitional region between the two first named parts. Inside the tooth is the *pulp cavity*, which is invaded by blood vessels and nerves through a passage remaining open at the base. The solid part of the tooth is threefold in character. The bulk of it is *dentine*, or ivory, a tissue denser than bone but like it permeated by tiny, radiating canals. Outside the dentine around the roots is what is known as the *cement*, or "substantia ossea," a bonelike substance that takes part in fixing the tooth in its socket, while over the

crown, wherever exposure to wear comes, the dentine is protected by a layer of *enamel*, which is the hardest, densest, most enduring part of the human body.

The composition of dentine and enamel in the human tooth is given by von Bibra, as follows:—

	Dentine	Enamel
Calcium phosphate and fluorid	66.72	89.82
Calcium carbonate	3.36	4.37
Magnesium phosphate	1.18	1.34
Other salts	0.73	0.88
Organic matter	28.01	3.59
	100.00%	100.00%

B. Development

About the seventh week in the development of a human embryo, certain Malpighian cells along the edge of the jaws where the future teeth are to be, start into accelerated activity, pushing down into the underlying dermal tissue in the form of the so-called *dental ridge* (Fig. 234). Along this ridge at intervals wherever a

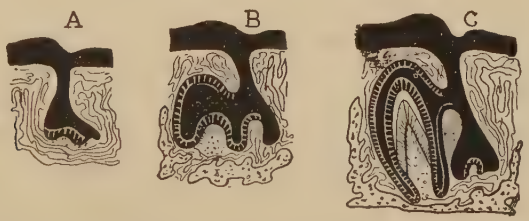


Fig. 234.—Three stages in the development of a tooth. *A*, formation of dental ridge; *B*, activity of ameloblasts; *C*, establishment of dental papilla. The epidermis is represented in black. (After Parker and Haswell.)

tooth is destined later to appear, groups of invading Malpighian cells become isolated by the absorption on all sides of their epidermal neighbors, so that they appear as conelike cups pointing outward, entirely surrounded by dermal cells. The cells lining these cups are called *ameloblasts*, and are destined to form the enamel that covers the crown of the teeth. Meanwhile, under each inverted enamel cup the dermal cells crowd together to form the *dental papilla*, of which the outer cells, known as *odontoblasts*, produce dentine that constitutes the bulk of the teeth, while

within the papilla there occurs an invasion of capillaries and nerve endings which are to occupy the future pulp cavity.

While the two substances, enamel and dentine, are being laid down side by side, the teeth take shape, their crowns eventually pushing through the surrounding tissues, and emerging so as to come into possible contact with the opposing teeth of the other jaw. This process of eruption is known as "cutting the teeth." Around the dentine of the embedded root of each tooth is deposited, through the activity of neighboring mesenchyme cells from the derma, the cement, or substantia ossea, which aids in fixing the tooth firmly in place in the jaw. Like the placoid scales of elasmobranch fishes with which they are homologous, teeth are compound structures, arising from ectodermal ameloblasts, mesodermal odontoblasts and mesenchyme cells. The horny, rasplike teeth of the jawless cyclostomes are entirely ectodermal structures and are not homologous with the teeth of other vertebrates.

C. Number

Lower vertebrates usually have an indefinite number of teeth, but in mammals the number becomes limited and definite. Generally speaking a reduction in the number of teeth is a mark of evolutionary advance associated with terrestrial life, less food, more chewing, shorter jaws, and stronger muscles of mastication, whereas an increase in the number of teeth, such as occurs secondarily in dolphins and other toothed whales, may be regarded as a reversion to ancestral conditions in connection with aquatic life, more abundant food, and less need of mastication.

There are some toothless species representing every class of vertebrates. Among fishes may be mentioned the sturgeon, *Acipenser*, and the sea horses and pipefishes (Lophobranchii). *Coregonus wartmanni*, a whitefish native to Lake Constance in Switzerland, is a toothless member of a large family of toothed fishes (Salmonidæ), although this aberrant species has transient embryonic teeth.

Toads, and among urodeles *Siren* at least, are toothless, while frogs have no teeth on the lower jaw.

Of reptiles the entire order of Chelonia, which includes turtles and tortoises, are without teeth, although in *Chelone* and *Trionyx* a reminiscent dental ridge develops temporarily in the embryo, only to fade away as the horny beak becomes ascendant. Several

extinct fossil reptiles, for example, *Oudenodon*, *Baptanodon*, and *Pteranodon*, are likewise known to have possessed beaks instead of teeth.

The same is true of all modern birds. That this was not always the case, however, is shown by the presence of teeth in *Archæopteryx* and the cretaceous birds of Kansas, *Hesperornis* and *Ichthyornis*. Embryonic teeth, of which there is ordinarily no trace in birds, have been found in the tern, *Sterna*.

Among mammals, monotremes are without teeth, also the edentates, *Myrmecophaga* and *Manis*, and the large whales (Mystacocœti). All of these widely different toothless mammals, however, furnish embryonic evidence that, with respect to this characteristic, they are degenerate descendants of ancestors with teeth.

D. Succession

Most of the lower vertebrates are *polyphyodont*, that is, they have a succession of teeth throughout life. This is exemplified particularly in a shark or dogfish, where the reserve "understudy" teeth may be seen arranged in diminishing rows behind the line in active service at the edge of the jaw. The continuous gradation over the edge of the jaw between the serried rows of elasmobranch teeth and the placoid scales of the skin, points unmistakably to a common plan of structure and accounts for vertebrate teeth as modified scales (Fig. 156).

Mammals are typically *diphyodont*, that is, they have one replacement of so-called *permanent teeth* following the temporary *milk dentition*. Certain marsupial embryos show traces of a *prelacteal dentition*, located between the milk teeth and the lips, and sometimes in exceptional cases, mammals produce an additional partial replacement of the "permanent" teeth, that is, a *post-definitive dentition*, making a total of four successions, all of which suggests that the typical diphyodontism of mammals has been derived from the polyphyodont condition of the lower forms.

There is, moreover, a tendency among mammals towards a still further reduction to a *monophyodont stage*. Marsupials, for instance, retain all their milk teeth except the last premolars, and certain insectivores, like the moles, *Scalopus* and *Condylura*, never cut their permanent teeth, while bats and guinea pigs have so far foreshortened the normal procedure of tooth succession as

to shed their teeth *in utero*, coming into the world with their permanent teeth already established. The sirenians, the toothed cetaceans (Odontocœti), and some rodents may also be described as *monophyodont*.

In man the eruption of the milk teeth is ordinarily accomplished in about eighteen months, while their replacement by the permanent dentition is normally completed at about the end of eighteen years, although an individual frequently carries representatives of both generations of teeth simultaneously for some time. The milk teeth differ from the permanent teeth by their smaller size, whiter color, and shape, being more constricted in the neck region, and having a greater spread of the roots in the case of the back teeth.

E. Situation

While the teeth are primarily located on the jaws, in fishes and other aquatic animals particularly, they occur attached to various skeletal foundations within the mouth cavity, such as the vomer, palatine, pterygoid, and parasphenoid, or even on the sides of the tongue, on the hyoid arch, and the gill arches. In reptiles and mammals they are usually confined to the jaws, although in some snakes and in the primitive New Zealand lizard, *Sphenodon*, they occur also in the roof of the mouth on the vomer and palatine bones.

Teeth of the upper jaw are interspaced with reference to those of the lower jaw. In man the large median upper incisors bite against not only the median but also the lateral incisors of the lower jaw, and every other tooth of the upper jaw, except the last molars, bites against the corresponding tooth of the lower jaw and also the tooth behind it.

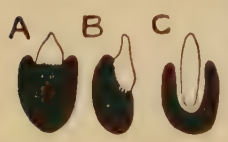


Fig. 235.—Types of attachment of teeth to jaws. *A*, acrodont; *B*, pleurodont; *C*, thecodont. (After Wiedersheim.)

F. Attachment

The manner in which teeth are attached to their skeletal support is dependent upon the degree to which the roots are developed. The simplest type of attachment, termed *acrodont* (Fig. 235), occurs in teeth essentially without roots, that are anchylosed directly to the edge of the jaw or other bony foundation. Such teeth may be broken off easily, and are polyphyodont. In some cases they are hinged on by a ligamentous base and may be folded down when not in use. The pike and

hake among fishes, as well as many kinds of snakes, have hinged teeth. Fishes as well as amphibians generally, are acrodont.

An improvement over the acrodont method is seen in certain lizards, where not only the base but one side of the tooth is involved in attachment to a shelf like ledge along the inner margin of the jaw (Fig. 236). By this method, which is called *pleurodont*, the blood and nerve supply goes in at the side instead of at the tip of the root.

FIG. 236.—Pleurodont teeth on the jaw of a lizard. (After Hilzheimer.)

The highest type of tooth has well developed roots, and is set in bony sockets in the jaw, a method of attachment known as *thecodont*, by which the capillaries and nerves enter the pulp cavity through the open tips of the roots. Some reptiles are thecodont, the alligators and crocodiles particularly, but this type of tooth attachment is especially characteristic of mammals, in some of which the teeth have progressed much beyond the primitive grasping function, and consequently require a stronger anchorage than is afforded by either the acrodont or pleurodont methods. The incisor teeth of gnawing rodents are so deeply set in bony sockets of the jaws, for example, that they become very effective tools, as may be seen in the case of the beaver, *Castor* (Fig. 237), which in its engineering operations can cut down large trees with these teeth.

FIG. 237.—Teeth of a rodent, *Geomys*, showing *diastema*, or toothless space in jaw between incisors and molars. (From Weber, after Bailey.)

G. MOVEMENT

There are three types of movement possible to teeth set in jaws, namely, orthal, lateral, and propaiinal, as brought out by

the muscles of mastication. The *orthal*, and commonest, type is vertical, and consists mostly in lifting up the lower jaw. Just as in a nutcracker, the farther back towards the angle of the jaw the work is done, the more powerful is the effect. The *lateral* type of movement is well exemplified by the ruminants which chew the cud with a sidewise motion, while the *propalinal* movement, which is "fore and aft" in direction, is practised by horses, elephants, and rodents. In the case of snakes with their sharp, backward-pointing prehensile teeth, the propalinal movement serves to pass along relentlessly the struggling prey down the throat. In fact it works so automatically that a snake would find it impossible, or very difficult, to eject a mouthful once started in the propalinal mill.

H. Differentiation

According to their degree of differentiation, teeth are described as isodont or heterodont. When practically all alike they are called *isodont*, but if they have undergone differentiation to serve a variety of uses such as gripping, cutting, tearing, or crushing, they are known as *heterodont*. The teeth of primitive water-dwelling vertebrates are commonly isodont, usually pointed, and adapted to serve as prehensile organs. Ordinarily the lower vertebrates with isodont teeth gulp their food whole. In evolutionary history, heterodontism arose with the occasion for chewing. The back teeth near the hinges of the jaws where the leverage is greatest, become modified into grinding *premolars* and crushing *molars*, while the front teeth, notably in the case of rodents, become specialized into cutting chisels, or *incisors*, to divide the food into morsels of convenient size for the grinding mill of the back teeth. Probably the most ancestral and the least changed of all heterodont teeth are the cone-shaped *canines*, or "eye-teeth," which are like the pointed grasping teeth of the lower forms. On either side of the canines, modification has taken place progressively and in divergent fashion, as indicated by the arrows, (Fig. 238), on the one hand towards the more chisel-like type of the incisors, on the other, towards that of the flat-topped premolars and molars.

The heterodontism of carnivores (Fig. 239), is characteristically different from that of herbivores. In the former case the sharp edges of the anterior grinders fit past each other like shears, for

cutting up animal food, the canines are prominent while the back molars tend to become degenerate. In the latter type it is the more anterior teeth that show degeneration, the canines usually being absent, while the posterior teeth near the hinge of the jaw become flattened, so as successfully to crush seeds, fruits, nuts, and herbage that come their way. A brown bear, which lives largely on an herbivorous diet, has the back molars well developed, while a polar bear, feeding exclusively on fishes, possesses efficient shearlike premolars and degenerate back teeth.

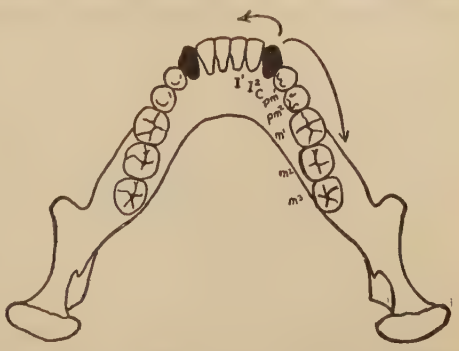


FIG. 238.—A human jaw, showing by arrows the two general types of differentiation in teeth from the primitive pointed canine teeth represented in black. *m*, molar; *pm*, premolar; *i*, incisor.

It is not unlikely that the gigantic cave bear, *Ursus spelæus*, whose bones have been found in suspicious proximity to those of cave men, was not a bloodthirsty terrorizing beast, but a harmless clumsy planteater, if we can believe the testimony of its teeth.

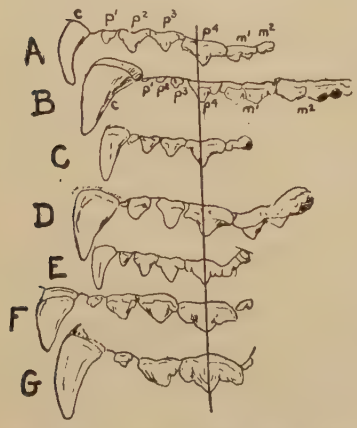


FIG. 239.—Teeth of the left upper jaw of various carnivores. *A*, dog; *B*, bear; *C*, martin; *D*, badger; *E*, mongoose; *F*, hyena; *G*, lion. (After Boaz.)

The molars of ruminants present a flat, grinding surface further diversified by crescentic ridges of projecting enamel, alternating with softer dentine. Since the dentine wears away more rapidly than the enamel ridges, the surviving enamel is constantly kept with sharp edges, and a rasplike abrasive surface on the grinding teeth is maintained. Such crescentic-surfaced teeth are said to be *selenodont* (Fig. 240). Similar enamel ridges are present on the molars of elephants, but they are arranged in transverse lines

instead of in crescents, making washboard-like teeth, described as *lophodont* (Fig. 241). They are particularly effective in connection with the propalinal movement of the jaws.

Fig. 240.—Selenodont dentition, or molars with crescentic surfaces of hard enamel.

In man and some other animals, the grinding surface of the molars is raised slightly into rounded tubercles and, being entirely covered with enamel, wears away more evenly. This is the *bunodont* type of teeth. It is illuminating to know that some of the ancestral elephants, such as *Palæomastodon*, for example, were bunodont, while their more specialized descendants of today, have become lophodont.

Fig. 241.—Grinding surface, partly worn, of right upper molar of African elephant. (After Owen.)

Finally, to add two more "donts" to this descriptive vocabulary of the teeth, the term *brachydont* describes teeth with short crowns and long roots, as in man, while the term *hypsel-odont* characterizes teeth with short roots and long crowns, such as are found in the dentition of the horse.

I. Dental Formulæ

In the case of different species having heterodont teeth it is useful to express the degree of their diversity in some convenient and compact form. This is accomplished by means of *dental formulæ*. For example, the permanent dentition of man may be expressed as follows, $\frac{2.1.2.3}{2.1.2.3}$, in which the figures above the horizontal line indicate in order from left to right the number of incisors, canines, premolars, and molars on the right side of the upper jaw, while the figures below the line stand for the corresponding teeth in the lower jaw. It is unnecessary of course to

indicate the teeth of the left side, which are like those on the right side except in reverse order.

The short-tailed monkeys (Catarrhini) of the Old World, have the same dental formula as man, but the long-tailed monkeys (Platyrhini) of the New World, have an additional premolar all around, making their formula $\frac{2.1.3.3}{2.1.3.3}$, with a total of thirty-six.

Some other dental formulæ are as follows: raccoon, $\frac{3.1.4.2}{3.1.4.2}$; bear, $\frac{3.1.4.2}{3.1.4.3}$; cat, $\frac{3.1.3.1}{3.1.2.1}$; pig, $\frac{3.1.4.3}{3.1.4.3}$; mouse, $\frac{1.0.0.3}{1.0.0.3}$; squirrel, $\frac{1.0.2.3}{1.0.1.3}$; cow, $\frac{0.0.3.3}{3.0.3.3}$; horse, $\frac{3.1.3.3}{3.1.3.3}$; opossum, $\frac{5.1.7.0}{4.1.7.0}$.

In herbivores the canine teeth are missing, or much reduced, leaving a toothless space, the *diastema* (Fig. 237), between the canines and premolars. The canines are relatively so small in the horse that a practical diastema exists, furnishing the space where the bits of the harness are held.

J. Unusual Teeth

Sometimes a pair of teeth will develop excessively, forming *tusks*. These may be either incisors or canines and are more likely to appear in the male than in the female, although both sexes of elephants and walruses have tusks. The largest known tooth is the tusk of an extinct mastodon, a specimen of which, that is in the American Museum of Natural History in New York City, measures over eleven feet in length. The wild boar strikes upward with tusks formed from modified canines of the lower jaw, while the male "dugong," or sea cow of the Red Sea, *Halcore* makes the effective blow from above downward with tusks evolved from the upper incisors. The babirusa, *Phacochœrus*, or wild hog of Celebes, has four upward-curving tusks, which are transformed canines of both jaws, those of the lower jaw piercing the upper lips.

In general tusks, as well as the prominent cutting incisors of rodents, retain a large opening at their base into the pulp cavity, insuring an abundant blood supply and consequent continued growth to compensate for the wearing away of the crown to which these exposed teeth are subjected. Such teeth in a way may be compared to angora hair in their manner of continuous growth.

In rodents the incisors are faced with enamel only on the anterior side, and so, being of unequal hardness, wear away more rapidly behind than in front, constantly leaving a sharp cutting beveled edge of enamel. When a rodent is so unfortunate as to break an incisor, leaving the opposing incisor no tooth to wear against, the animal usually meets eventual death by starvation, because the unhindered growth of the surviving tooth often reaches such an extent that the mouth can no longer be properly closed, and feeding becomes impossible.

The male narwhal, *Monodon* (Fig. 71, C), has the upper left incisor prolonged enormously into a formidable twisted pikestaff with which it rams or impales its enemies, while the sawfish, *Pristis* (Fig. 19, C), carries a similar weapon in the form of an elongated rostrum, or snout, with laterally projecting teeth along the sides.

Among poisonous snakes one or two of the anterior teeth may develop into *fangs*, which are either grooved or hollow. Whenever a fang is struck into another animal the secretion of the poison gland is pressed out through the hollow or groove into the wound.

A so-called *egg tooth* is present as a transitory structure in the embryo of snakes and lizards. It is situated in a median position at the tip of the lower jaw, and projects forward. The young reptile uses it like a can opener to hatch itself out of the imprisoning shell. According to Röse, a pair of egg teeth is initiated in the embryo of the viper, *Vipera*, but only one becomes developed sufficiently to be of service, and this is shed soon after hatching.

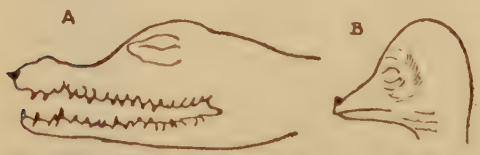


FIG. 242.—Transitory corneal egg tooth of, *A*, alligator; and, *B*, bird, which is used as a "can opener" in hatching out of the shell. (After Hilzheimer.)

There is also a corneal "egg tooth" of horny texture on the tip of the beak of many birds, which, although not homologous with the egg tooth of reptiles, nevertheless serves the same purpose. It may be seen still adhering to the tip of the beak of young chicks which have just hatched into the world (Fig. 242, B). A similar emergency tool is present in the lizard *Sphenodon*, and in the Crocodilia (Fig. 242, A), and Chelonia, as well as the monotremes which are the only mammals that hatch out of an eggshell.

K. Origin of the Molars

There are two theories to account for the origin of molar teeth. First, the *concrescence theory* of Röse and others, assumes that they are products of the fusion of separate, primitive, coneshaped teeth. The posterior teeth in the jaw of *Sphenodon* present evidence for this point of view. The other, and more widely accepted explanation, is the *differentiation theory* of Cope and Osborn, which postulates the growth of additional contact surfaces, or *cusps*, upon the crown of an originally conical tooth (Fig. 243). This theory is based largely upon evidence presented by the ancestral teeth of fossil mammals.

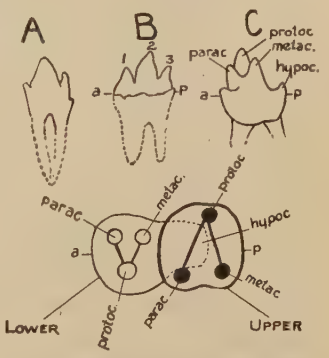


Fig. 243.—Plan of molar teeth. *A, Microconodon; B, Triconodon; C, Amphitherium. a*, anterior; *p*, posterior; *hypoc.*, hypoconus or hypoconid; *metac.*, metaconus or metaconid; *parac.*, paraconus or paraconid; *protoc.*, protoconus or protoconid. (After Osborn.)

The possible number of definite cusps, or contact surfaces, seems to be six, of which the point of the primitive conical tooth, or *protoconus*, is the oldest. Lateral to the protoconus are two other cusps, the *paraconus* in the anterior position, and the *metaconus* posterior to the protoconus. These cusps are usually connected by ridges with the protoconus between, making the *tritubercular* tooth which is the characteristic molar of mammals generally from the earliest representatives down to Eocene times. Even today the mole, *Chrysochloris*, and certain other insectivores, as well as the opossum, *Didelphys*, and some lemurs, exhibit this ancestral tuberculate type.

When the three "conuses" lie in a straight line parallel to the edge of the jaw, the teeth are termed *tricodont*, but usually they zigzag, assuming a triangular position with relation to each other, with the protoconus on the inside, and the paraconus and metaconus placed towards the outer margin of the jaw, in which case they are described as *trigonodont*. In more highly developed molars additional cusps appear, which have been designated as the *hypoconus*, *talonus*, and *entoconus*. All of these descriptive terms ending in *-us* apply to cusps on molars of the upper jaw. The corresponding cusps upon the molars of the lower jaw are

designated by the termination *-id*. Thus, in a tritubercular molar of the lower jaw the cusps are *protoconid*, *paraconid*, and *metaconid*, respectively, of which the latter two are on the inside position in trigonodont dentition, while the protoconid is placed towards the outer margin of the jaw, which is just the reverse of the relative location of their opponents of the upper jaw into which they fit.

It is quite likely that both the concrescence and the differentiation theories may be needed to explain all the facts, both embryological and palæontological, that are known about the origin of the "double" teeth, as neither explanation is quite sufficient when taken alone.

L. The Trend of Human Teeth

The teeth of ancient man show certain differences from those of man today, which possibly give some suggestion as to the future evolution of human dentition. The jaws in which teeth are set are becoming shorter and less prognathous, with the result that the teeth of modern man are more crowded and less regular. Also caries, or decay, is more common in the teeth of modern civilized man than in the teeth of his prehistoric ancestors, where it was practically unknown. Wiedersheim reports upon evidences of decay in teeth, after an examination of a large number of skulls from various museum collections, as follows: Esquimaux, 2.5 per cent; Indians, 3–10 per cent; Malays, 3–20 per cent; Chinese, 40 per cent; Europeans, 80–100 per cent.

In primitive man the upper incisors came into opposition edge to edge with the lower incisors, and were frequently worn flat in consequence, while in modern man there is a tendency for them to shut past each other like the blades of a pair of shears.

The "wisdom teeth," or the third molars, are apparently doomed. They are the last to appear and the first to go. Frequently they remain uncut, or do not develop a grinding surface. In prehistoric man, however, they were plainly in evidence, and they are usually well developed in negroes, mongols, and aboriginal Australians. The upper lateral incisors, and the second molars, also show evidences of being degenerate structures, failing to appear in a considerable number of cases.

IV. PROGRESSIVE ZONE

1. Pharynx

The pharynx includes the stretch of digestive highway from the posterior part of the mouth cavity to the beginning of the esophagus. While its actual extent is relatively small, its diversity of function, and consequently the degree to which it is modified in various vertebrates, is very great.

There are two quite different streams of material traveling through this gateway, namely, food and air. In fishes they both enter the mouth together (Fig. 244, A), and proceed in parallel course without mutual interference, the food passing straight to the esophagus where it continues on its way, while the air, dissolved in water, passes out over the gills that hang in the lateral gill slits, which like portholes pierce the sides of the pharynx. The paired nasal pits on the snout of a fish do not open into the mouth cavity, and have nothing to do either with the pharynx or with breathing.

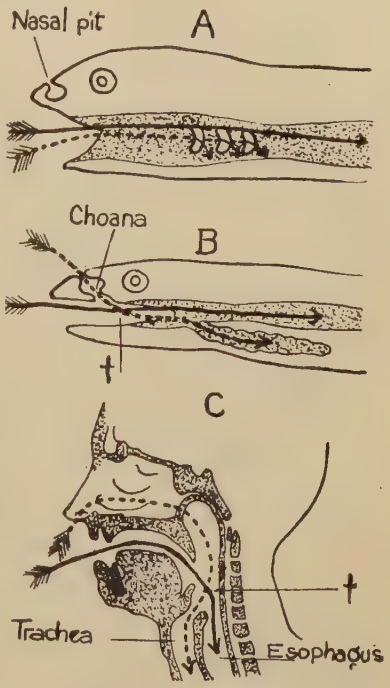


FIG. 244.—Diagrams of the evolution of the pharyngeal chiasma. *A*, fish; *B*, reptile; *C*, man. The solid arrows indicate the course of the food, and the dotted arrows the course of the air. The position of the chiasma in man is pushed back as the result of the development of the hard palate. (After Wiedersheim.)

In Amphibia, the first land forms which began to possess lungs and to breathe free air, the nasal pits deepen until they break through into the mouth cavity, forming a respiratory passageway called the *choana* (Fig. 244, B). This allows air to pass to the lungs without the necessity of opening the mouth, and thus exposing its lining to disastrous drying up.

As the free air is taken into the cavity through the choana with

the mouth closed, it is forced back into the lungs by means of the throat muscles, a process which would be quite impossible with the mouth open as the air could then escape in the wrong direction. Embryologically the lungs are ventral outgrowths from the floor of the pharynx, and thus, while the food takes a straight course from mouth to esophagus as in fishes, the air, entering the nostrils dorsally, crosses the path of the food and is forced ventrally into the lungs. Vertebrates above the Amphibia, that is, reptiles, birds and mammals, have developed a hard palate, or secondary roof of the mouth, carrying the internal openings of the choanæ backward so that the crossing of the ways now transferred to the pharynx, comes to be called the *pharyngeal chiasma.*

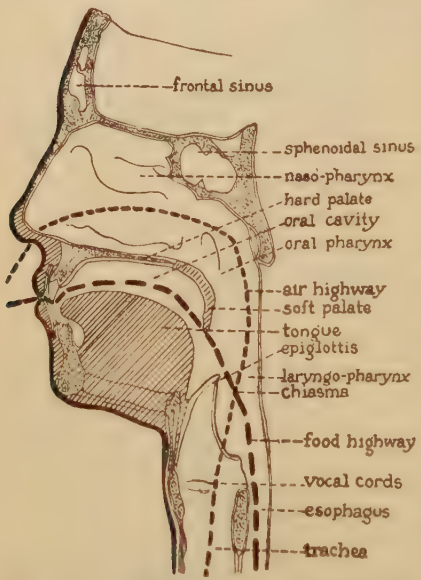


FIG. 245. — Sagittal section through the head and throat, to show the pharyngeal chiasma. (Drawn by Martha Whitmarsh.)

This chiasma necessitates the establishment of various anatomical modifications (Fig. 245), that, like traffic officers at a busy street crossing, regulate the traffic and prevent confusion, but which add materially to the expense of maintenance. The *epiglottis*, for example, is introduced as a trapdoor to guard the entrance into the trachea whenever food passes by, in order that it shall not go the wrong way. There are developed in the entire pharyngeal region also a variety of adaptive glandular or lymphoid structures, particularly the *tonsils*, having a wide range of functions, and forming the seat of so many complications and troubles, both structural and physiological, that physicians and surgeons specializing in this field alone, have their busy hands full.

It may be pointed out that if the choanæ in man had passed through the chin instead of the nose, avoiding the pharyngeal chiasma entirely, some present troubles would have been elimina-

ted at least, although with such a drastic change other difficulties would have been introduced. In any case the pharyngeal chiasma clearly stresses the fact that our anatomical machinery is the result of successive modifications rather than of *de novo* specifications, and that the moral from comparative anatomy as well as from other aspects of life, is that one should seek to make the best of his inheritance, whatever it is, rather than vainly to regret not having been endowed with perfection in the beginning.

In man the pharynx is a somewhat funnel-shaped cavity about five inches long, without an anterior wall and extending from the base of the skull to the level of the sixth cervical vertebra, where it narrows into the esophagus. Instead of having an anterior wall it communicates directly with three cavities, one below the other, which suggests the division of the pharynx, for purposes of description, into the naso-pharynx, oro-pharynx, and laryngo-pharynx.

The *naso-pharynx*, which is not concerned with alimentary traffic but is entirely respiratory in function, is separated by the soft palate from the oro-pharynx below. In general it retains a definite contour, since its walls are practically stationary with the exception of the palatine floor which can be somewhat elevated and depressed. On either side of the naso-pharynx opens a *Eustachian tube* from the chamber of the middle ear. These tubes are the anatomical successors of the first pair of gill slits between the mandibular and hyoid arches of ancestral aquatic forms.

The *oro-pharynx* communicates through the *isthmus of the fauces*, or the posterior opening of the oral cavity, directly with the oral cavity itself, below which is the base of the tongue that here assumes a vertical position and practically reduces the oro-pharynx to a transverse slit when the mouth is closed. On the sides of the oro-pharynx are located the *palatine tonsils*, two masses of glandular, lymphoid tissue. On the vertical face of the base of the tongue there is also lymphoid tissue, known as the *lingual tonsils*, while upon the posterior wall of the naso-pharynx still more of this tissue forms, the *pharyngeal tonsils*, which when enlarged are popularly called "adenoids," so that an incomplete ring of tonsilar tissue surrounds the pharyngeal passage-way, of which the lateral palatine tonsils are the most prominent.

The *laryngo-pharynx*, continuous with the oro-pharynx, is the

lower part of the pharynx between the larynx and the esophagus. It includes the critical region of the pharyngeal chiasma. Except during the passage of food, which slips down either side of the closed glottis, the laryngo-pharynx is collapsed into a narrow slit.

Thus it will be seen that the pharynx as a whole, like a colonial kitchen, opens into many possible regions. It has communications, in fact, through seven different openings, as follows: two choanæ and two Eustachian tubes in the naso-pharynx; the isthmus of the fauces in the oro-pharynx; and, in the laryngo-pharynx, the glottis and the esophagus.

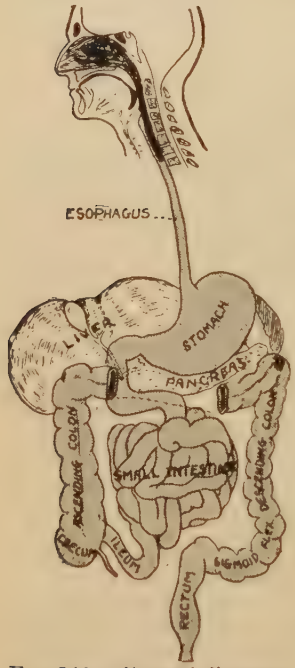


FIG. 246.—General diagrammatic view of the digestive system in man. The transverse colon has been cut to show the duodenum, but its course is indicated by dotted lines. (After Cunningham.)

The pharynx serves as a point of departure for describing the respiratory system, since it is the region of the gills of fishes and amphibians, as well as the point of origin for the swim bladder of fishes and the lungs of land animals. This respiratory sidetrack of the pharynx, however, will be avoided until the chapter upon *Respiration*. Consideration of the numerous pharyngeal glands, such as the thyreoid, parathyreoid, thymus, epithelial corpuscles, and post-branchial bodies, will also be taken up later in the chapter on *Endocrine Glands*.

2. Esophagus

Over the entrance of the esophagus might well be written Dante's immortal line: "*All hope abandon, ye who enter here*," for in the course of it the muscles of its walls pass from a voluntary to an involuntary nerve control. Ruminants are exceptional in that they have voluntary nerve fibers extending the whole length of the esophagus and are, therefore, able to regurgitate the cud at will for more prolonged chewing.

The esophagus, a short, comparatively unmodified part of the digestive tube between the pharynx and the stomach (Fig. 246), is primarily a sphincter, the office of which is to forward the food

by peristalsis beyond normal control. The peristaltic action of the walls of the esophagus is well shown by a horse drinking at a brook, for the gulps of water taken have to travel up hill. In the case of a snake the violent peristalsis necessary in swallowing a comparatively large mouthful, such as a frog, is supplemented by the muscles of the body wall.

When not in use the esophagus contracts to modest dimensions, but upon occasion it is capable of great temporary expansion. In many vertebrates its inner lining is characterized by expansive longitudinal folds, while in marine chelonians it is beset with backward-projecting, horny papillæ, which help these animals to swallow the slippery seaweeds upon which they habitually feed.

The length of the esophagus is dependent largely upon the presence or absence of a neck. In frogs and toads the neck is reduced to a minimum so that a fly which enters the mouth of one of these animals finds itself almost immediately landed in the stomach, whereas in long-necked animals, such as a giraffe, for example, the esophageal adventures of the food are much more extended. In adult man the length of the esophagus is approximately fourteen inches, the lower end of it piercing the diaphragm to enter the body cavity before joining the stomach.

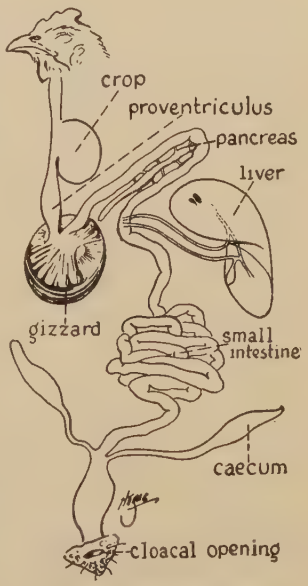


Fig. 247.—Digestive tract of a hen.

A noteworthy differentiation of the esophagus in birds is a lateral enlargement, known as the *crop* (Fig. 247). This may serve simply as a convenience for the temporary storage of food, hastily secured in the presence of competitors or enemies, as in the case of seedeaters generally, or it may be supplied with glands which act chemically upon the food, as in scratching birds, pigeons, and some others. The secretion produced in the crop of a pigeon is called "pigeon's milk." It is a cheesy, nutritious substance and is fed to the nestlings by regurgitation.

Among the lower vertebrates any external line of demarcation

between the esophagus and stomach is either absent or vague, but in birds and mammals there is usually a definite point of transition.

3. Stomach

The stomach is a conspicuous enlargement of the digestive tract lying between the esophagus and the intestine (Fig. 248).

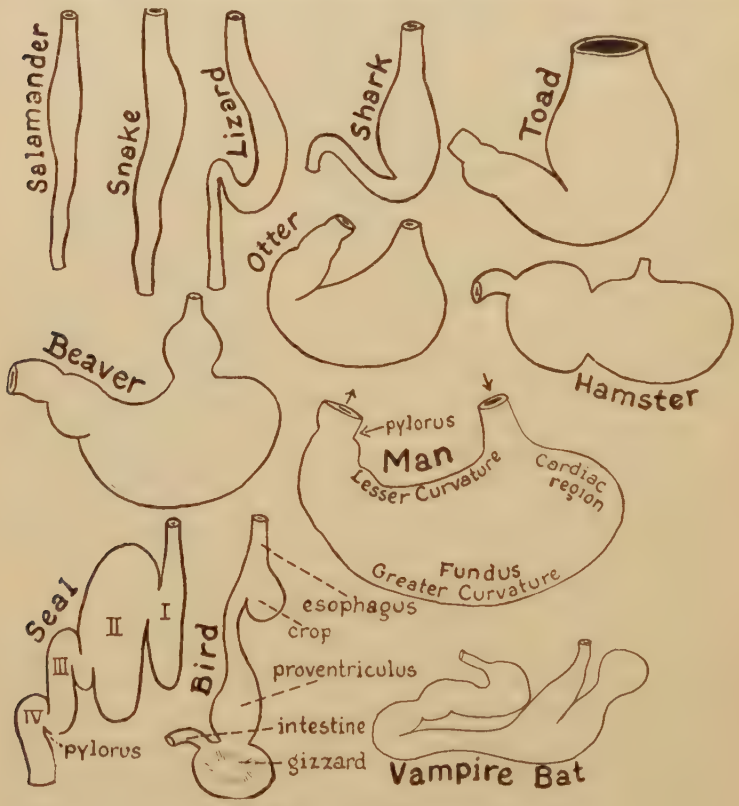


Fig. 248.—Different stomachs.

Originally in certain fishes and salamanders, it is spindle-shaped, and arranged to conform with the general contour of an elongated body, but eventually, in the higher vertebrates, it becomes saclike in shape, assuming a somewhat transverse position in the body cavity. Between these extremes may be found many gradations of form and position.

In the dogfish, for example, the stomach, instead of being a

primitive, straight, spindle-shaped enlargement with the entrance and exit at opposite ends, is doubled back as a U-shaped tube, so that the two ends are brought close together side by side. Stomachs in the form of a bent tube occur also in the flounder, haddock, salmon, carp, sturgeon, sole, and many others.

In some fishes, such as the perch, smelt, bullhead, whiting, and herring, the loop becomes fused along its inner bend in such a way that a bag-shaped pouch, or *fundus*, is formed, with the entrance and exit near together at one side. This type of stomach, when shifted into a transverse position, is much like that of man, with a *lesser curvature* on the upper side between the entrance and exit, and a *greater curvature*, forming the longer contour around the outer margin or former elbow of the stomach.

The entrance of the stomach is somewhat larger than the exit and is less distinctly marked off, although the lining of the digestive tract itself in the region of the esophagus is easily distinguished from that of the stomach, even when the transition from one part to the other externally is extremely vague and indefinite.

The exit of the stomach is closed by the *pyloric valve*, a fold of mucous membrane reinforced by a sphincter muscle, which relaxes temporarily for the passage of food into the intestine only when the proper stimulative password is given. The walls of the stomach are muscular enough to insure the movement of the food around and around by peristalsis until it has been reduced, by mixture with secretions, to a proper consistency and degree of acidity. Then, as it is presented at the closed pylorus, the sphincter muscle relaxes, and small, successive amounts of properly qualified mixture are allowed to slip through into the intestine.

Amphioxus and larval cyclostomes, which have not gone far enough in evolution to develop peristaltic muscles, have the entire digestive tube lined with cilia, according to Schimkewitsch, the mission of which is to keep the food moving along. In the human fetus also, as a possible reminder whence man came, the posterior part of the stomach lining is clothed with cilia.

There is a tendency for the stomach to become differentiated into two or more regions, distinguished from each other by location and function. Thus, in the U-shaped stomach of the dogfish, one speaks of a *cardiac limb* and a *pyloric limb*, while in certain mammals, the mouse, for example, a constriction in the middle of the stomach marks off a cardiac chamber from a pyloric chamber.

Medical literature contains numerous references to the occasional occurrence of so-called "hour-glass stomachs" in man (Fig. 249), which bear a strong resemblance to the two-chambered stomachs of mice and certain monkeys (*Hylobates* and *Semnopithecus*). Whether such abnormal structures in man are pathological or ancestral, is uncertain.

Fig. 249. — So-called "hour-glass stomach" in man. (After Wiedersheim.)

An extreme modification of the subdivision of the stomach into chambers is reached by the ruminants, which have four "stomachs" (Fig. 250). The first in order is the *rumen*, or "paunch," which is a spacious storage bag for the temporary reception of the grass or herbage upon which ruminants feed. From the rumen the freshly garnered food is passed over unmodified into the *reticulum*, or "honeycomb stomach," which as its name indicates, is lined with many pits. Here it is compacted into cuds that, when leisure from feeding comes, are regurgitated into the mouth, where they are chewed over and mixed with saliva until sufficiently Fletcherized to slip past the passageway to the rumen and, upon being swallowed again, into the *omasum*, or "many plies stomach." This third chamber is lined with many folds and communicates with the *abomasum*, or true glandular stomach, where the food is mixed with gastric juices and chemically modified before being forwarded into the intestine.

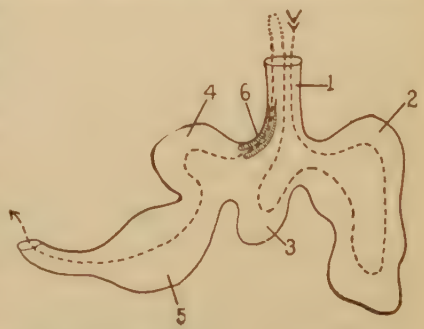


Fig. 250.—Diagram of a ruminant stomach, with dotted lines showing the course of the food. *1*, esophagus; *2*, rumen; *3*, reticulum; *4*, omasum; *5*, abomasum; *6*, valves that permit a small slippery cud to enter the omasum, but which are crowded back against the walls of the esophagus by any large unchewed mass of vegetation, closing the groove of the omasum so that the food-mass finds temporary storage in the large rumen. (After Hesse.)

The vampire bat, *Desmodus*, exhibits a peculiar adaptation with reference to its bloodsucking habits, the fundus of the stomach being drawn down into a deep elastic pouch (Fig. 248). When a vampire fastens on to a victim, it can fill this spacious reservoir with blood until the entire body is quite swollen in consequence.

The cardiac and pyloric regions of the stomach in birds have become separated into chambers very unlike each other in character (Fig. 247). The cardiac chamber becomes the *gizzard*, with a thick, muscular wall and a hard, horny lining. In this muscular mill the food is ground up, instead of by means of teeth, as in mammals. Gravel ("gizzard stones"), retained within the gizzard cavity, aids in the process of food attrition. The whole device is a part of the general program of centralization of parts which the birds, as adapted flying machines, have evolved. The highest differentiation of the gizzard is reached in seed-eating birds, and is least in evidence in birds of prey. The pyloric chamber which opens into the gizzard, becomes a *glandular stomach* where the food undergoes chemical modification before passing into the intestine.

Among reptiles the crocodilian stomach approaches that of birds in complexity, since a gizzard-like cardiac chamber receives the food before it passes over into a glandular pyloric sac, which corresponds to the chemically functioning stomach of other animals.

There are at least three functions performed by the stomach, namely, storage, mechanical manipulation, and chemical modification.

The advantages of *food storage* are obvious. Among the lower sedentary creatures, like sponges and clams, for example, there is no provision for storage, and feeding is practically a continuous process. As the necessity for hunting food arises, the consequent rivalry for daily bread and the adventurous escape from devouring enemies becomes more and more the daily program of animal existence. The need of seizing a sufficient supply of food in a minimum of time and then retiring to safety or to engaging in other activities is, therefore, apparent. By periodic, voluntary filling of a storage chamber with food, opportunity is left for other activities at the same time that the involuntary machinery of the body is faithfully attending to the contents of the stomach with meticulous deliberation and care.

The function of *mechanical manipulation*, or peristalsis, has already been mentioned. By this means the muscular walls of the stomach churn the food mass around, mixing it with digestive secretions. This movement may actually be seen upon a fluorescent screen when an animal, like a cat, whose food has been mixed

with bismuth subnitrate, is exposed to X-rays, since bismuth subnitrate is opaque to X-rays (Fig. 251).

The function of *chemical modification* is dependent upon the presence of glands in the lining of the stomach, which produce secretions of various kinds. In the region of the fundus, *gastric glands* are most numerous. These glands produce a certain amount of free hydrochloric acid, together with three kinds of enzymes, namely, pepsin, rennin, and gastric lipase, that do preliminary service in the chemical preparation of certain kinds of foods. Pepsin, which acts only in the presence of acid, breaks down proteins into simpler compounds; *rennin* coagulates the casein out of milk, rendering it capable of being changed by pepsin into soluble substances that undergo further changes farther along in the digestive tract; while *gastric lipase* begins the work of splitting up fats, but is not very pronounced in its activity.

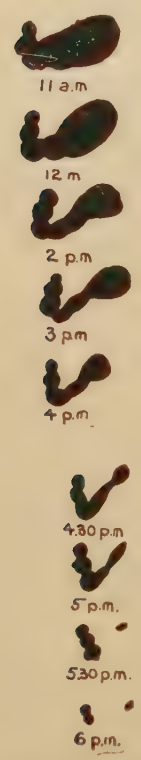


FIG. 251.—X-ray of the contents of a cat's stomach at successive intervals after being fed with bread and milk and bismuth subnitrate, which is opaque to the X-ray. (After Cannon.)

The lining of the stomach itself is not digested by its own secretions because its component cells are living and thus resistant to enzymatic action. This is the reason why a tapeworm lives and prospers while bathed in the digestive gastric juices of its host.

V. DEGRESSIVE ZONE

The intestine is a long lane with many turnings. In the higher vertebrates it is differentiated into a *degressive zone*, called the *small intestine*, in which the food substances passing through are largely diverted to the blood; and a shorter part, usually of somewhat greater diameter, known as the *large intestine*, that constitutes the *egressive zone* from which the unutilized residue of the food mass is ejected.

1. The Small Intestine

All other regions of the digestive tract are subsidiary in function to the small intestine. Here it is that the food mass, which has

been undergoing chemical and mechanical modification, is finally converted into a sufficiently soluble form to be passed over into the blood stream by osmosis, whence it is finally distributed to the uttermost needy cells of the body.

In amphioxus the entire lining of the digestive tract is composed of potentially absorbing cells, corresponding in function with the small intestine, with no enlargement that might properly be called either stomach or large intestine.

The straight, comparatively short intestine in *cyclostomes* is likewise undifferentiated, except for the presence of a longitudinal fold, the *typhlosole*, that increases its absorbing surface.

In elasmobranch fishes the typhlosole is much longer than the intestine itself, with the result that it becomes twisted into a *spiral valve* (Fig. 207). This makes an enlarged surface for the diversion of the food within a very compact space, since the intestine is shorter than the U-shaped stomach and is not bent. A spiral valve is also present in the intestine of the dipnoi, certain ganoids, and at least one exceptional teleost (*Chenocentrus*). Twisted *coprolites* (fossil feces), found with the bones of ichthyosaurs, indicate that these extinct reptiles might have been equipped with a spiral valve device that moulded the feces into a twisted shape.

The ganoids, as a class, show a different method of increasing the intestinal surface by means of *pyloric cæca*, which are sac-like diverticula at the junction between the stomach and small intestine (Fig. 209). Both spiral valve and pyloric cæca are present, although poorly developed.

The next step in the evolution of the small intestine is found in teleost fishes, which have given up the spiral valve idea and gone over entirely to the elaboration of pyloric cæca. In some of the bony fishes these structures form a large tuft of tubes, occupying considerable space within the constricted body cavity.

With amphibians the distinction between small and large intestine begins (Fig. 252). Increase of internal surface is gained by the elongation and coiling of the tube itself, rather than by typhlosoles, spiral valves, or pyloric cæca. Tadpoles, which feed upon vegetation, have an enormously lengthened intestine out of all proportion to the length of the entire body, while the intestine of the adult frog or toad, which lives on concentrated animal food, is relatively very much shorter and less coiled. In

the Amphibia, furthermore, the inner surface of the intestine begins to be diversified by villosities, which reach their greatest differentiation in the *villi* that characterize the small intestine of mammals.

The sluggish reptiles as a class mark off a definite large intestine, in which the feces are retained for a prolonged period within the digestive tract. At the junction between the small and large intestine a new diverticulum, the *colic cæcum*, appears, and pyloric cæca are no longer present. In turtles the colic cæcum is

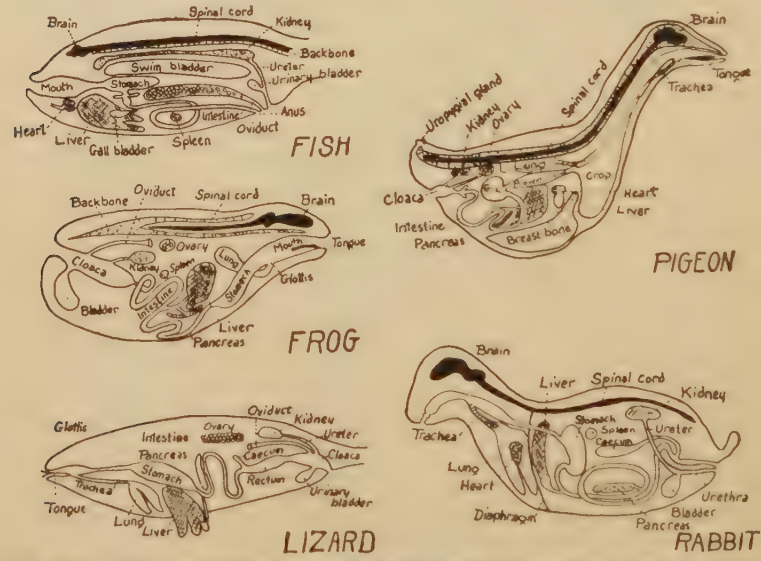


FIG. 252.—Diagrams of the internal plans of various vertebrate types. (After G. W. Herrick.)

hardly more than a swelling (Fig. 210), but it becomes more pronounced in other reptiles, while, owing to the elongated shape of the body, the small intestine in snakes is only slightly coiled.

The colic cæcum is small or wanting in monotremes, flesh-eating marsupials, carnivores, edentates, odontocœti, insectivores, and bats, but is very large in herbivores where it may even exceed the body in length.

The degenerate free end of the colic cæcum forms the *processus vermiformis* in certain rodents, cats, civets, monkeys, and man. According to Wiedersheim, the processus vermiformis in man varies in length from two to twenty-five centimeters, with an

average of about eight and one-half centimeters. It tends to shorten with age and to become closed in later life. Statistics on the closure of the processus vermiformis in 1,005 observed cases are given by Müller in percentages as follows:—

Age	♂	♀
1 to 10 years	2.0	0.0
11 to 20 "	5.1	5.4
21 to 30 "	6.4	8.7
31 to 40 "	12.7	23.8
41 to 50 "	26.2	34.8
51 to 60 "	20.5	30.0
61 to 70 "	29.3	50.0
71 to 80 "	38.7	26.0
81 to 90 "	53.3	52.9

Birds, which have evolved a long way from their reptilian forebears, have a much coiled small intestine, two colic cæca, and a large intestine which is decidedly fore shortened, since it is incompatible with the strenuous aërial life of birds to carry about the ballast of unnecessarily retained feces. A single colic cæcum appears in ostriches that is as capacious as all the rest of the small intestines, and it is made even more effective by the presence of a spiral valve.

In mammals the small intestine is commonly distinguishable from the large intestine, a single colic cæcum[1] marking the transition from one region to the other. Herbivores have a noticeably longer intestine than carnivores. The small intestine is divided more or less arbitrarily into *duodenum*, *jejunum*, and *ileum*, a distinction which, though first made out in man, applies to most other mammals. The duodenum, or the part next the stomach, is comparatively short; the jejunum which follows, as contrasted with the posteriorly located ileum, is longer, somewhat thicker-walled, richer in blood vessels and has a wider lumen.

The characteristic modification of the lining of the mammalian small intestine, is the presence of innumerable tiny, thickly-set velvety projections, or *villi*, which enormously increase in a minimum space the absorbing surface exposed to the dissolved food. In fact these are the degressive organs of absorption. Each villus consists of a thin wall of cells and contains within itself a

[1] Exceptions are *Trichechus*, *Hyrax*, and the edentates, *Dasypus* and *Myrmecophaga*, which have two.

capillary loop and a microscopic *lacteal*, or terminal element of the lymphatic system(Fig. 253).

In the ileum particularly, the forest of villi is frequently interrupted by irregular bare patches from half an inch to three or four inches in length, which show like worn places in the nap of a Brussels carpet.

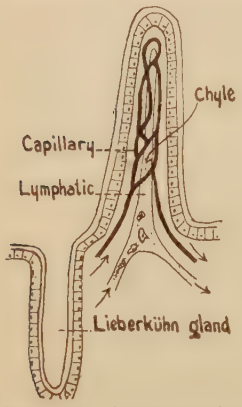


Fig. 253.—Diagram of a villus and a Lieberkühn gland on the side of a crypt.

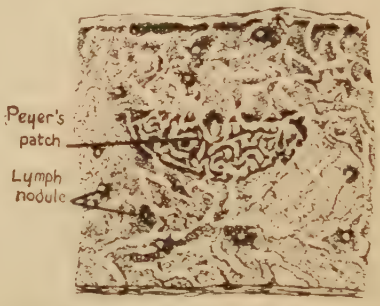


Fig. 254. —Surface view of a portion of mucous membrane of ileum, showing a Peyer's patch, and solitary lymph nodes. (After Piersol.)

These are the "intestinal tonsils," or *Peyer's patches* (Fig. 254). They are lymphoid in character and it is important to notice that in typhoid fever the chief lesions occur in these areas.

For some distance also, from near the pylorus to the middle of the ileum, the inner surface of the small intestine is thrown up into irregular transverse ridges, called the *plicæ circulares*, which, like the spiral valve, tend to slow down the passage of food and to facilitate its absorption by increase of surface.

2. Glands

Two conspicuous glands differing greatly in appearance, intimate structure, and function, but which are alike in being entodermal derivatives of the mesodæum (the embryonic forerunner of the small intestine), are connected with the anterior end of the duodenum just posterior to the pylorus. These are the *liver* and *pancreas*. They are so large that they extend entirely outside the digestive tube itself, occupying positions within the body cavity.

A. Liver

The liver is an older organ, both ontogenetically and phylogenetically, than the pancreas. It should not be confused with the

so-called "liver" of starfishes, crabs, molluscs, or other invertebrates, since it is in no way homologous with these structures. The vertebrate liver—and every vertebrate has a liver—is the "busiest port on the whole river of life." It is so voluminous that in man, for example, it may easily contain one fifth of all the blood, while several times an hour the entire blood supply of the body passes through its myriad capillaries, undergoing profound modifications by way of additions and subtractions of constituent parts.

It is not an organ of digestion, as popularly supposed, although it aids materially in the digestive processes by furnishing a favorable alkaline medium, the *bile*, in which the digestive enzymes produced by the pancreas, particularly those that metabolize fats, may act. In the bile itself there are no digestive enzymes.

The bile is a bitter alkaline fluid, about ninety per cent water, tinged with pigments from the wreckage of red blood corpuscles and containing salts, both organic and inorganic, and waste materials of different kinds. It is formed continuously and is poured into the duodenum through the bile duct, where it mingles with the food mass upon the escape of the latter through the pylorus into the intestine, contributing materially to the excreta that pass out of the alimentary canal. The bile arising in the liver may amount to a pint or a pint and a half daily in man. When an excess of bile is produced it may be temporarily stored in the *gall bladder*, a reservoir-like enlargement of the bile duct. This duct drains the liver and is termed the *hepatic duct*, as distinguished from the *cystic duct* that comes from the gall bladder. When these two ducts join to empty into the intestine, the common duct thus formed is called the *ductus choledicus* (Fig. 255).

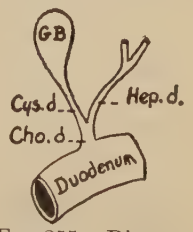


FIG. 255.—Diagram of the liver ducts. *cys. d*, cystic duct; *cho. d*, choledical duct; *GB*, gall bladder; *Hep. d*, hepatic duct. (After Nuhn.)

In addition to the excretion of bile, the liver produces also to some extent a waste product from the breakdown of nitrogenous foods, the *urea*, which subsequently is eliminated from the blood through the kidneys.

Still another use of the liver is the temporary storage of surplus food. When carbohydrate foods, which have been transformed into soluble sugars and incorporated into the blood stream, reach the strainer-like capillaries of the liver, any surplus beyond what

is required for the immediate fuel needs of the working muscles, is temporarily stored in the form of *glycogen*, or "animal starch." This reserve can be changed back into a soluble sugar, *dextrose*, and poured into the blood stream upon demand.

Among the various functions of the liver, therefore, are included the production of bile, containing various excretory by-products such as cholesterol, inorganic salts and pigments; the breakdown and, at least during embryonic life, the formation of red blood corpuscles; the secretion of organic bile salts which stimulate digestion; the partial antisepsis of the intestinal contents through the presence of the bile; the temporary storage of glycogen and fat; the conversion of stored foods back into soluble and usable form; and finally, the continuous regulation, quantitative and qualitative, of the constituents of the blood. In this latter function of balancing the food ration of the blood, the liver principally serves the organism of which it is a part. Dr. Woods Hutchinson says of the liver: "It is altogether the most useful and desirable citizen, and withal a cheerful and even convivial one, mixing our drinks, putting the stick into our vitamine cocktails, and the sugar and cream into life's coffee."

The liver is an adaptive space filler, consisting usually of two or more lobes. Its shape and size are conditioned, first, by its voluminous blood vessels, nerves and "ligaments," or connective tissue attachments; second, by neighboring organs which crowd it; and third, by the confining walls of the body cavity and the diaphragm. In mammals the two larger lobes are separated by what is known as the *umbilical fissure*, as determined by the *round ligament*, representing the atrophied remains of the umbilical vein. A large *portal fissure* marks the gateway for the blood vessels, ducts, and nerves that pass to and from the liver in adult life.

With every breath that expands the neighboring lungs, and because of the uneasy peristalsis of the stomach and intestine pressing upon it, the flexible lobes of the liver are constantly slipping slightly over each other, changing meanwhile somewhat in shape for adjustment to the varying conditions of available space.

In structure the liver is made up primarily of glandular cells, polyhedral in shape largely by reason of being crowded together, and in close contact with capillaries (Fig. 256). They have an elaborate system of drainage ducts, and an adequate nerve supply. The whole mass is embedded and encapsuled in a supporting net-

work of connective tissue, with bandlike strands for attachment within the body cavity, and for the safe convoy of blood vessels, ducts, and nerves. Along the approximated sides of each two neighboring gland cells (Fig. 257), appear tiny intercellular spaces or grooves like the spaces between the fingers when two fists are placed together. These capillary ducts which are formed as indenting intercellular grooves, that permeate the entire liver-mass, are compounded with others in an ever enlarging array, finally emerging as the large, *hepatic duct* which combines them all.

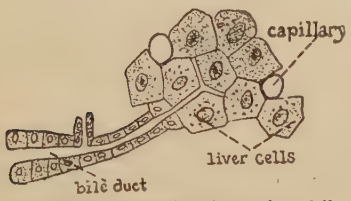


FIG. 256.—Termination of a bile duct between liver cells. (After Huxley.)

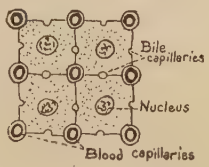


FIG. 257. — Diagram of four adjacent liver cells. (From Jordan and Ferguson, after Merkel.)

The system of blood capillaries or sinusoids that also enmeshes the gland cells, is independent of the network of drainage tubes. It is unlike the blood supply of most organs in that there are two sources from which the entering blood is derived, namely, the *hepatic artery* which brings blood from the heart in the same way that all other organs of the body are supplied by some artery, and the *portal vein* that comes freshly laden with food from the intestine, on its way to the heart to be eventually sent to all the organs of the body. The capillaries derived from both the hepatic artery and the portal vein hopelessly lose their identity as they combine within the liver to form the *hepatic veins*, which drain the blood of the liver into the heart.

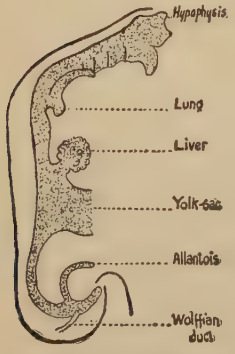


FIG. 258.—Reconstruction of the alimentary canal of a 4.2 mm. human embryo. (After His.)

Embryologically the liver is a hollow ventral outgrowth near the beginning of the intestine just anterior to the embryonic yolk sac (Fig. 258), between the two vitelline veins. It lies at first between two layers of ventral mesentery in the *transverse septum* from which the diaphragm is in part produced, but eventually it becomes

so large that it projects some distance into the body cavity, pushing a covering of endothelial serosa with it.

An entodermal outgrowth from the gut itself becomes the secretory, glandular part of the liver, and this soon becomes enmeshed with the vascular mesenchyme from the transverse septum and the neighboring blood vessels, to form the liver tissue. As this tissue grows forward, particularly in the anterior or cranial region of the transverse septum, the posterior or caudal region, which is the primary point of origin, develops the ducts and gall bladder.

In amphioxus the liver remains a single sac projecting forward (Fig. 13), and beset with capillaries which bring food from the intestine, much as in the early embryonic phase of higher forms. It is lined with ciliated glandular epithelium, and secretes a digestive fluid. In most vertebrates, however, the liver has typically two lobes although lampreys and snakes, perhaps on account of their elongated body form, have only one lobe. The liver is relatively larger in carnivores than in herbivores, a fact no doubt connected with the presence of more fat in the diet of the former. In certain carnivores, such as dogs and weasels, for example, there are as many as seven lobes present. The original tubular plan of the gland, as found in fishes and lower vertebrates, thus becomes masked or obliterated by the anastomosis of the component lobules. In man five lobes are described (Fig. 259). The *right lobe* is the largest, constituting about four-fifths of the entire mass, while the wedge-shaped *left lobe* is next in size, separated from the former by the *round ligament*. On the inner aspect between these lobes is a square *quadrate lobe* near the gall bladder, and the so-called *Spigelian lobe* between the postcaval and portal fissures, with a small *caudate lobe* connected with the Spigelian lobe.

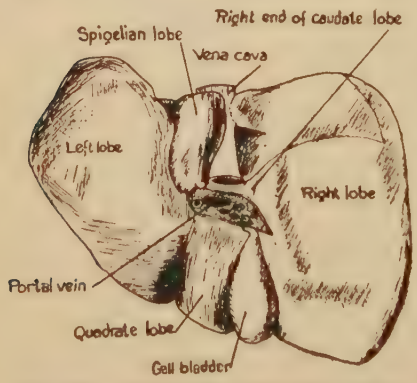


FIG. 259.—The human liver from behind. (After Cunningham.)

The *gall bladder*, which seems to be an emergency device for

animals that digest a considerable amount of fatty food, is absent in many planteaters. The human gall bladder is pear-shaped and holds about one and one half ounces of bile. Its total absence, as well as the abnormal presence of two gall bladders, has been noted in man.

"Gall stones" are concretions of cholesterol and other solid constituents of the bile, frequently with the addition of a limy deposit, which sometimes appear in the gall bladder. When large they are comparatively harmless, but if small they may block the ducts, thus forcing into the tissues a harmful diversion of the bile which is being constantly secreted.

The cystic duct especially lends itself to such obstruction since it is modified within by mucous folds, forming the *Heisterian valve*, which make the blocking of the passage-way easier than as if the lumen of the duct was not thus obstructed. Moreover, the choledical duct penetrates the wall of the intestine at such a slant, that continued pressure from within, such as may result from prolonged constipation, may mechanically close the duct temporarily, causing abnormal disposition of the bile.

B. Pancreas

The pancreas is a compound alveolar gland of irregular shape, usually to be found lying in the fold between the stomach and the duodenum. It is the second largest gland of the vertebrate body and projects into the body cavity from the point of its embryonic connection with the digestive tube, although in the lamprey, *Petromyzon*, and in certain teleosts, it may remain embedded in the wall of the intestine.

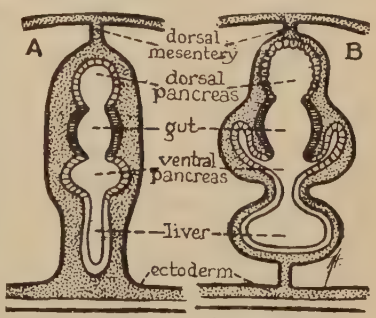


Fig. 260.—Origin of pancreas and liver. (After Schimkewitsch.)

It arises as one or more entodermal outgrowths from the embryonic gut just posterior to the liver. These outgrowths are usually three in number of which one is dorsal and two are ventral in position (Fig. 260). The latter fuse together into a common gland, while the ducts formed at each point of outgrowth may either persist, or, as is more often the case, may dis-

appear with the exception of one (Fig. 261). The ducts of the ventral components are called *Wirsung's ducts*, while that of the dorsal pancreas is named the *duct of Santorini*. In some forms these ducts unite either with each other to make a common duct, or with the bile duct. In lampreys all the ducts are lost, the secretion of the pancreas consequently becoming entirely endocrine, that is, distributed by the blood rather than poured directly to the outside or into some passage-way.

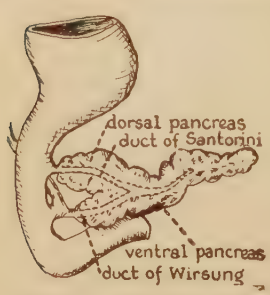


FIG. 261.—Diagram of the double pancreas in a human embryo of five weeks. The *duct of Wirsung* persists as the permanent pancreatic duct. (After Kollmann.)

In general it may be said that the pancreas is a gland of dual character, since, in addition to its production of digestive pancreatic juice that is poured into the intestine through ducts, there are present in the pancreatic tissue certain distinct intertubercular cell aggregates, also entodermal in origin, called the *islands of Langerhans* (Fig. 262), which secrete substances of a character quite different from the pancreatic juice itself, that are carried to all parts of the body through the circulating blood. Which of these two kinds of secreting cells, the original entodermal outgrowths from the embryonic gut, or the islands of Langerhans, represents the original pancreatic material, and whether one has, or has not, been derived from the other by modification, is still a matter of controversy. It may be pointed out that the islands of Langerhans are invariably present in all true vertebrates and are undoubtedly early settlers if not the first inhabitants, whereas the other secreting cells are wanting in certain vertebrates. For instance, there is no trace of a pancreas in amphioxus, and in elasmobranch fishes only the dorsal pancreas

FIG. 262.—Pancreas of rabbit. *e.p.d.*, epithelium of pancreatic duct; *i L*, island of Langerhans. (After Krause.)

develops, with its *ductus Santorini*. In sturgeons the pancreas is made up of two dorsal and two ventral components with only the right ventral duct remaining. Moreover, in bony fishes and the lower vertebrates generally, the pancreas is primitive in character, being widely diffuse and irregular in form. Among mammals also there is great variety in the form, position, and size of this important gland. A single surviving pancreatic duct is found in man, *Wirsung's duct*, connecting with one of the ventral embryonic components.

Three enzymes that aid in the digestive processes are furnished by the pancreatic juice, namely, *amylopsin*, which like the ptyalin of the saliva acts upon carbohydrates; *trypsin*, which modifies proteins; and *steapsin*, which breaks up fats. These three digestive enzymes, therefore, are prepared to render the three fundamental kinds of food, carbohydrates, proteins, and fats, fit for transference through the blood to all parts of the body. In man about a pint and a half of such digestive pancreatic juice is poured daily into the intestine. The activating substance, or *hormone*, that is diverted from the islands of Langerhans into the blood, has to do with the utilization of sugar in the tissues, and its failure to be produced in sufficient quantity results in diabetes.

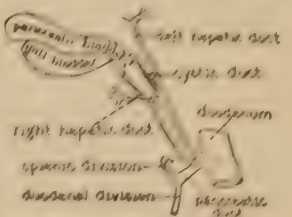


FIG. 263. "Pancreatic bladder" from a female cat. (After Boyden.)

A curious modification of the pancreatic apparatus which not infrequently appears, particularly in the cat, is the *pancreatic bladder* or reservoir-like enlargement of the pancreatic duct for the temporary storage of excessive secretion, an organ quite comparable with the gall bladder that serves as a safety valve for the liver (Fig. 263).

C. Intestinal Glands

In addition to the liver and pancreas, the secretions of which are mixed with the food in the duodenum, there are numerous smaller glands occupying the walls of the intestinal tract, that likewise make chemical contributions essential to digestion in the form of an intestinal juice, *succus entericus*.

Among mammals there are at least two kinds of intestinal

glands, known as *Brunner's glands* and the *glands of Lieberkühn*. The former are more in evidence in herbivorous mammals than in carnivores, their occurrence being greater at the pyloric end of the duodenum than at its posterior end where the ducts from the liver and pancreas enter the tube. They produce an acid secretion that is chemically somewhat like that of the gastric glands of the stomach.

The glands of Lieberkühn, which produce an alkaline secretion, are vastly more numerous and extend throughout the entire length of the small intestine, particularly from the duodenal region on. They are arranged not only around the bases of the *villi*, which carpet the floor of the intestine, but also occupy the walls of tiny sunken pits, or *crypts*, which are interspersed among the villi like deep gorges between steep mountains. These crypts (Fig. 253) increase the surface of the small intestine and are to be regarded only as mechanical devices for surface enlargement rather than as essential parts of the glands themselves.

In the epithelium of the duodenum, according to Bayliss and Stirling, there is produced under the chemical stimulation of the acidulated food mass, or *chyme*, that enters the intestine from the pyloric opening of the stomach, a "hormone," called *pancreatic secretin*, which is carried by the blood to the pancreas where it excites that gland into activity. This reaction occurs only when food enters into the intestine, otherwise the pancreatic juice, if continuously produced, would much of the time be wasted. The three pancreatic enzymes, amylopsin, trypsin, and steapsin, being ineffective in an acid medium such as is produced by the action of the gastric glands of the stomach and by the less effective Brunner's glands in the duodenum, it becomes necessary to change the acid food mass to an alkaline character before these indispensable agents of digestion can do their work. It seems, therefore, to be the mission of the innumerable Lieberkühn glands, aided by the bile from the liver, to change the intestinal food content from an acid to an alkaline character, so that the pancreatic enzymes will have a suitable medium in which to perform their function.

In addition to the three pancreatic enzymes, the succus entericus contains certain enzymes of its own which play a part in the complicated chemical preparation of the food for its absorption

into the blood. Thus, *enterokinase* is an activating agent that is particularly effective in stimulating trypsin to do its work on protein foods; *maltase* splits sugars, and *erepsin* and *nuclease* are still other known enzymes produced by the intestinal glands which take part in accomplishing the marvel of transmuting one organism along the food route into the substance of another.

From the reptiles on and particularly in the mammals, the lining of the small intestine is further characterized by the presence of elongated lymphatic areas or patches of reticular connective tissue, *Peyer's patches*, in which lymphocytes are enmeshed, and over which the villi are absent. These patches, which have already been mentioned in connection with the ileum, facilitate the absorption of certain components of the liquefied food.

VI. EGRESSIVE ZONE

The large intestine constitutes the egressive portion of the alimentary tract through which the residue of the food mass is forwarded for expulsion after the usable part has been diverted through the walls of the small intestine into the blood. Its diminished importance in the essential work of the alimentary tract may account in part for the relative absence of structural modifications designed to increase its inner surface.

Except in the embryo it is without the villi which characterize the small intestine and, although Lieberkühn glands are present along its endothelial lining in lessening numbers, glandular secretions are not so much concerned with chemical digestion as with the mechanical lubrication of the feces, from which the water content has been largely withdrawn into the blood stream.

In man the large intestine is about five feet in length and is differentiated into the *colon*, with *ascending*, *transverse*, and *descending* parts, and the *rectum*, ending at the anal opening (Fig. 246). The colic cæcum and the processus vermiformis, already mentioned, also belong to the large intestine. The same distinctions characterize the large intestine of many mammals but are not so apparent in other vertebrates, since only the rectum of mammals is homologous with the large intestine of lower vertebrates. In the pipefish, *Sygnathus*, the stickleback, *Gasterosteus*, and some other fishes, the "large intestine" is actually smaller than the small intestine.

In man the colon, which is arched around the coiled small

intestine, is characterized by three narrow bands of longitudinal muscles, the *tæniæ coli*, that pull this part of the intestine together so as to form three rows of pouches, or *haustra*, along its entire length, a modification present in varying degree in the large intestine of other mammals.

Attached to the external wall of the haustra there are also many little processes of connective tissue, usually distended with fat, called the *appendices epiploicæ* (Fig. 213), but neither the haustra nor the appendices epiploicæ extend to the rectum.

In birds the rectal region of the large intestine is notably reduced. Since it is a disadvantage for these aërial creatures to carry about an unnecessary weight of useless fecal material, the provision for its temporary retention is curtailed, the excreta being disposed of as rapidly as they are produced.

Metchnikof, as well as others, has pointed out that the large intestine in man, particularly in the rectal region, is a danger zone, a veritable "sewage swamp," because bacteria of various kinds flourish upon the undigested residue of the food there retained, contaminating the body constantly with the fermentive and toxic by-products of their metabolism. In a tabulation of 1,148 cases of cancer of the alimentary tract, eighty-nine per cent were located in the susceptible region of the rectum. There are some obvious advantages to mankind in possessing a voluminous rectum where excreta may be temporarily held so that their evacuation may be timed and controlled more readily than is the case with flying birds, although the disadvantages are far from negligible. It is somewhat difficult to see how such an unfortunate evolutionary acquisition could have been fostered by natural selection, but the fact that it reaches its greatest elaboration in herbivorous mammals where it is still useful in caring for plant foods rich in cellulose, may give some hint of why such a danger zone came to be acquired and preserved in man.

Fig. 264. — Anal canal and lower part of the rectum, split open to show anal valves and sphincter muscle. *a.c.*, anal canal; *a.v.*, anal valves; *rec.*, rectum; *sp.m*, sphincter muscle. (From Cunningham, after Birmingham.)

In the lower vertebrates including the monotremes among mammals, the rectum opens into the *cloaca*, which is a postanal

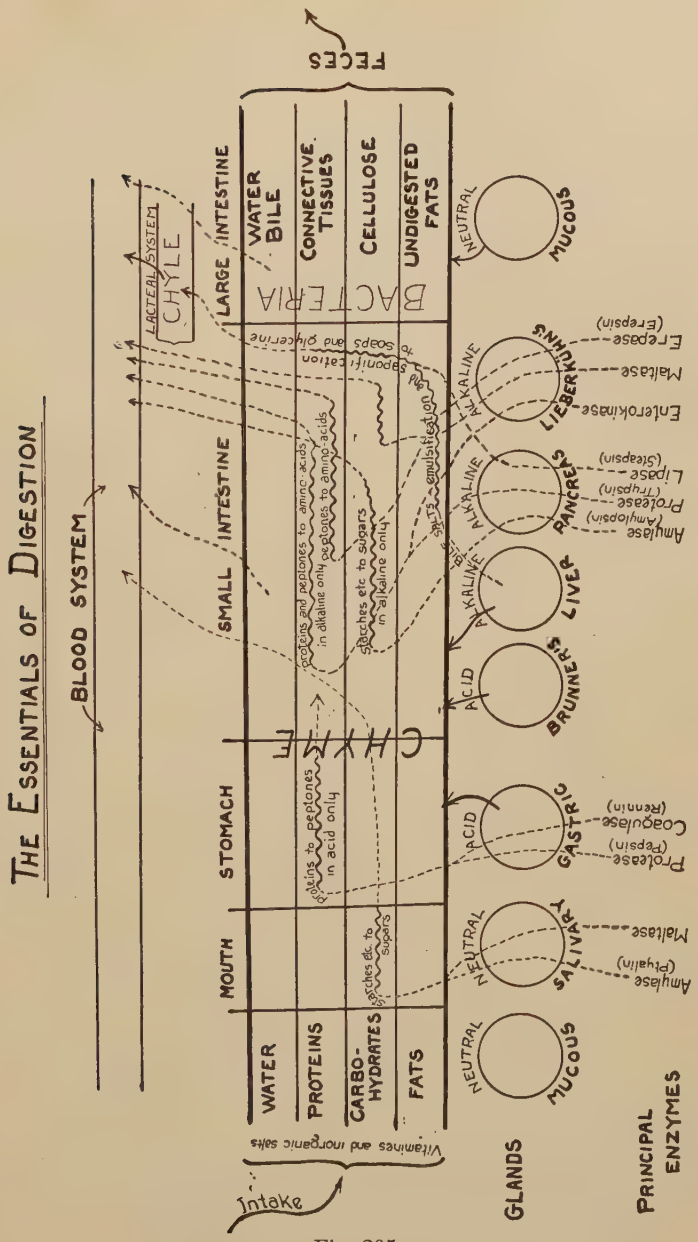

THE ESSENTIALS OF DIGESTION
BLOOD SYSTEM
LACTEAL SYSTEM
CHYLE
FAECES
MOUTH
STOMACH
SMALL INTESTINE
LARGE INTESTINE
CHYME
WATER
PROTEINS
CARBO-HYDRATES
FATS
Vitamines and inorganic salts
Intake
WATER
BILE
CONNECTIVE TISSUES
CELLULOSE
UNDIGESTED FATS
BACTERIA
proteins to peptones in acid only
starches etc. to sugars
proteins and peptones to amino-acids in alkaline only
starches etc. to sugars in alkaline only
saponification to soaps and glycerine
fats emulsification
NEUTRAL
ACID
ALKALINE
MUCOUS
SALIVARY
GASTRIC
BRUNNER'S
PANCREAS
LIEBERKÜHN'S
LIVER
GLANDS
Amylase (Ptyalin)
Maltase
Protease (Pepsin)
Coagulase (Rennin)
Amylase (Amylopsin)
Protease (Trypsin)
Lipase (Steapsin)
Enterokinase
Maltase
Erepase (Erepsin)
PRINCIPAL ENZYMES

Fig. 265

chamber receiving not only the feces from the digestive tube but also contributions from the genital and urinary ducts. The rectum ends with the *anus*, which is closed by a sphincter muscle under control of the will unlike the other circular muscles of the digestive tract that accomplish segmentation and peristalsis under involuntary control.

The inner walls of the rectum in man are modified by two or three transverse crescentic shelflike folds, the *rectal valves* (Fig. 264), which are doubtless adaptations to erect posture, since they are absent in quadrupeds where the feces do not weigh against the anal sphincter.

VII. THE ESSENTIALS OF DIGESTION

A summary of the chemical adventures of food during its passage through the digestive tube, is shown in the appended diagram (Fig. 265).

The blood stream receives the food from the small intestine after it has been reduced to absorbable, liquid form. This reduction is partly mechanical, but it involves above all things a chemical breakdown that is actuated by enzymes. The irregular lines in the diagram indicate the particular glands from which each enzyme arises, and, at the wavy interval of the line, the general locality in the digestive tract where it is effective and the kind of food involved in each case.

CHAPTER XII

INTERNAL TRANSPORTATION (CIRCULATORY SYSTEM)

I. IN GENERAL

The circulatory system is the mechanism that attends to the needful transportation of various substances within the organism. Not only are food, water, and air taken into the animal body, but these indispensable substances are also delivered to each living cell wherever located, otherwise life would cease. Moreover, the waste products which are inevitable in the metabolic processes common to all living things, must be collected for elimination from every cellular nook and cranny of the body, and transported either directly to the outside or to passages leading to the outside.

In microscopic unicellular animals, internal transportation is accomplished by the movement of the cytoplasm within the cell itself. It is easy to see how particles of matter, once introduced into a protozoan like *Ameba*, for example, whose insides flow like cold molasses, may shift their position within the cell body. This intracellular cytoplasmic movement, which is the most primitive kind of a circulatory system, is entirely adequate for bodies of microscopic mass, and always remains as the final essential phase of circulation even in organisms built up of countless cellular units, since intake materials must not only reach each individual cell, but become incorporated and circulated therein as well.

In many-celled forms, however, most of the component cells do not have direct surface exposure to the environment. The only way food, water, and air can enter such organisms and penetrate to their ultimate parts, is either through, or between, the cells that form the body. The passing of materials *through* from one cell to another by osmosis is so slow and indirect a method that the ultimate cell in the line receives only what is left after all the intervening ones have taken their toll. It is a great improvement, therefore, when passageways are opened up *between* the cells so that materials may be forwarded freely, thus reaching the ultimate cells directly and easily without repeated osmotic

manipulation. The same sort of an advance in efficiency is seen when fire fighters substitute a hose line for a makeshift hand to hand "bucket brigade."

The circulatory system proper may be briefly described as consisting of such a series of passage-ways throughout the body, together with a fluid vehicle, both blood and lymph, for transporting various materials, and lastly, a mechanism for sending this fluid through the channels.

II. BLOOD AND LYMPH (THE CARRIERS)

1. General Uses of the Blood

Mephistopheles, in Goethe's "Faust," is biologically correct when he exclaims: "*Blut ist ein ganz besonderer Saft!*" (Blood is a very peculiar fluid.)

In the first place it is not a lifeless fluid, but a *circulating tissue*, made up of detached, living cells floating in a liquid plasma and capable of metabolic changes. The fact that it moves about marks it off distinctively from all other tissues.

It is conspicuously kaleidoscopic in character, changing constantly in its intimate composition as it passes through the different parts of the body, for it is not only the common carrier *to* the various tissues of everything needful for their maintenance, but also the collector *from* the tissues of the products of metabolism. In the last analysis cells of every type in the animal body contribute something to the blood and receive something in return, so that the blood reflects the entire metabolism of the body. In spite of this fact, however, it is normally kept at nearly a constant level of component parts. When serious deviations occur, like the excessive loss of water from the blood during cholera, or of blood cells in anæmia or hemorrhage, pathological consequences are sure to follow.

In general the following functions, at least, may be performed by the blood:—

A. Equilibration of the Water Content

Water is not only a fluid that facilitates the internal transport of materials, making good losses by evaporation and otherwise, and preventing local drying up of tissues, but it is also the great solvent of various substances throughout the body. The degree of activity exhibited by any tissue is directly dependent upon the

fluidity of the cytoplasm within its cellular units, and this in turn is ultimately a matter of water supplied by the blood.

B. Liberation of Energy

Tissues "burn" in the presence of oxygen, thus releasing energy. This release of energy is what constitutes "living." Some tissues, like muscles, for example, lend themselves particularly to this process, while others, such as skeletal tissues, resemble more the iron girders of a fireproof building, and do not burn as readily. The oxygen necessary for the release of stored energy is delivered to the tissues of vertebrates by the hæmoglobin in the red corpuscles of the blood.

C. Distribution of Food

The blood is, from one point of view, a solution or emulsion of food substances carried in the plasma, or perhaps also to some extent as solid particles engulfed in the white blood cells. It is thus the grocery delivery boy for the cellular community.

D. Regulation of Temperature

Body temperature which results from the oxidation of the tissues, is equalized by means of the circulation of the blood, much as in a heating plant equipped with hot water pipes. Such equalization is necessary because of the unequal production of energy, in the form of heat, by different tissues of the body.

In so-called "warm-blooded" animals the body temperature is maintained at a practically constant level, regardless of the temperature of the environment, thus enhancing the animal's independence. In "cold-blooded" animals, on the other hand, owing partly to the oxygen-carrying capacity of the blood, the temperature of the body fluctuates in response to the surrounding temperature, and the animal is consequently a thermal slave to the environment in which it finds itself. It has been demonstrated, however, that even cold-blooded fishes when ill may show a fever-like temperature.

E. Transmission of Chemical Substances

Hormones, which are chemical messengers from the endocrine glands, perform metabolic feats frequently at some distance from their point of origin, traveling along the blood highways. Drugs and poisons introduced into the organism, likewise gain ready dispersal over the body through the blood. This is why a person

with malaria, for example, feels "sick all over," since the blood carrying the organisms producing malarial poison literally goes over the whole body.

F. Defense against Parasitic Invasion

Troublesome foreign invaders, such as infective bacteria and protozoa, are regularly combated by the phagocytes of the blood which devour them. The cures of most diseases that are "caught," depend upon the successful outcome of this function of the blood.

G. Disposal of Cell Wreckage

The blood is a perpetual funeral cortège, in which are being borne away the "ashes" of dead cells, foreign bodies, bacterial products, and the wastes of metabolism generally. The manner of this elimination will be considered in Chapter XIV.

H. Chemical Elaboration

Furthermore, the blood is a peripatetic laboratory in which chemical transformations of wide variety are constantly going forward, as, for example, the formation of antitoxins of various sorts, or the production of glycogen from the blood in the liver.

I. Clinical Diagnosis

All the functions of the blood thus far indicated have to do with personal physiological benefits but blood may also be useful, outside the individual which elaborates it, in identifying disease. No other tissue gives so good a flashlight picture to the diagnostician of the present state of the varying metabolism of the body as the blood. The ease with which a sample may be obtained for examination without injury to the patient, and the readiness with which deviations from the normal are revealed therein, have resulted in an increasing dependence upon the blood as a means of clinical diagnosis. For example, in a doubtful case of either typhoid fever or appendicitis, the examination of the blood furnishes an immediate differential diagnosis, since in typhoid the number of white blood cells is below, while in appendicitis it is above normal. There is no doubt that dependence upon blood examination will become greater as technique is perfected and new approaches to the study of the blood are developed.

2. Amount of Blood

In adult man the amount of blood is about seven or eight per cent of the total weight, that is, about ten pounds or five quarts,

for a person weighing 130 pounds. In a newborn child the percentage of blood is less than in the adult, about five per cent of the total weight, while in lower vertebrates the relative amount of blood is also less than in mammals. Haempel gives the quantity of blood in fishes as less than two per cent of the total body weight.

The blood supply is temporarily increased in those organs that are active as, for example, in the stomach immediately after eating, or the small intestine during digestion.

As to specific gravity, blood is heavier than water. For man the figures have been given as 1.041 to 1.067.

3. Erythrocytes

Our sanguinary forebears were well acquainted with the appearance of blood, for the pages of history are copiously stained with it. Not until 1696, however, about two centuries after Columbus had discovered America and his adventurous bones had returned to dust, did the Hollander, Anthony van Leeuwenhoek, find with his primitive lenses, that blood is "composed of exceeding small particles." These he named "globules," which he said "in most animals are of a red color, swimming in a liquor, called by physicians the serum," and further that "by means of these globules the motion of the blood becomes visible, which otherwise would not be discoverable by the sight."

Red corpuscles are peculiar to vertebrates. The unquestionable first appearance of these characteristic globules in the evolutionary series is in cyclostomes. In amphioxus and larval eels they are wanting. Whenever invertebrates show red blood, as, for example, the blood clam, *Arca*, or "blood worms," (the larvæ of the midge *Chironomus*), the hæmoglobin that produces the color is not located in red corpuscles for these are absent, but is found to be dissolved in the plasma.

Red corpuscles, or *erythrocytes*, as they are technically known, are directly concerned with the respiratory function. The exchange of gases involved in respiration is accomplished, as has already been mentioned, by means of the chemical pigment *hæmoglobin*, which is present inside of the corpuscles.

Hæmoglobin has the power both of temporarily loading up with oxygen, when it becomes *oxy-hæmoglobin*, and of readily releasing its load of oxygen, usually after transportation, wherever oxygen is absent. Hæmoglobin is said to have the power of ab-

sorbing seventy times as much oxygen as the plasma of the blood, which can carry oxygen only in solution. In man about one-third of each red corpuscle, or approximately fourteen per cent of the entire mass, is hæmoglobin. The peculiar ability of this substance to carry the amount of oxygen necessary in breathing may be destroyed by the action of certain poisonous gases, such as carbon monoxide, if encountered, for example, from the exhaust of a running automobile engine in a closed garage. When such an accident occurs recovery may follow if enough unaffected erythrocytes remain to maintain life until new corpuscles are elaborated or added by transfusion.

The erythrocytes of most vertebrates are oval discs that appear to bulge in the center on account of the presence of a nucleus (Fig. 266). Among mammals erythrocytes are more circular in outline and, with a strange exception in the case of camels, the nucleus disappears, either by a process of absorption, extrusion, or budding, while the cell itself becomes a degenerate sac, or *stroma capsule*, having an internal structure very little understood, but containing a concentrated solution of hæmoglobin. The original name "corpuscle," (small body) therefore, fits the erythrocyte with more accuracy than the modern designation of "red blood cell."

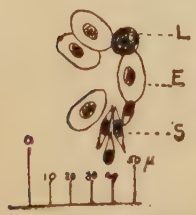


Fig. 266. — Camera lucida drawings of blood cells in frog. *L*, lymphocyte; *E*, erythrocyte; *S*, spindle cell. (After Krause.)

In size the erythrocytes range from seventy-five micra[1] in the urodele *Amphiuma*, to two and one-half micra in the muskdeer, *Tragulus*. Some other reported measurements of blood corpuscles are as follows: mud puppy, 58 μ; turtle, 25 μ; lamprey, 15 μ; eel, 15 μ; chick, 12 μ; elephant, 9.4 μ; man, 7.5 μ.

In general, the smaller corpuscles are, the more surface they expose for a given quantity of blood, and consequently the more effective they are in respiration. One of the factors determining the "cold-bloodedness" of the lower vertebrates as contrasted with mammals, is the larger relative size of their erythrocytes, and the smaller relative surface of exposure to oxygen.

The *number* of erythrocytes in the blood is of considerable clinical importance. In man it is normally about 5,000,000 per cubic millimeter for the male, 4,500,000 for the somewhat less

[1] A micron equals 1/1,000 of a millimeter.

metabolic female, while in the highly metabolic infant the count is greater than in either adult. The number in every case increases with a decrease of atmospheric pressure, as, for instance, in high altitudes. This is why patients who are combating tuberculosis sometimes go to high altitudes where the lessened pressure of the rarefied air demands more surface exposure of hæmoglobin to accomplish the normal amount of respiration, thus forcing the body to curative effort by producing more red corpuscles in compensation.

The total number of red corpuscles in the average human being has been estimated at twenty-five billions, a number quite incomprehensible. Counting continuously at the rate of 200 per minute, it would take 250 years to complete the tally. This amazing figure may be visualized by stating that the total respiratory surface of the erythrocytes in a normal individual has been computed as equal to an area of approximately 3,000 square meters, a surface ample enough for laying out four regulation baseball diamonds side by side.

Hæmolysis, the wearing out or destruction of erythrocytes, is the inevitable outcome of their strenuous existence. The amount of coloring matter present in bile, which is due principally to the hæmoglobin of broken-down erythrocytes, furnishes to the physiologist an index for estimating that the probable normal length of life for a single blood cell in man is only about ten days. On this basis, since the total number of twenty-five billion erythrocytes is approximately maintained throughout life, it becomes necessary that new red blood be manufactured at an average rate of about 30,000 cells per second.

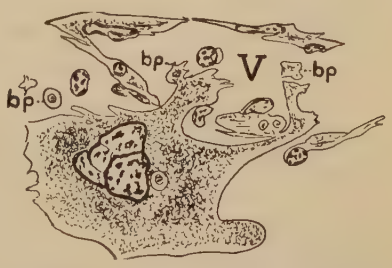


Fig. 267.—Giant cell from the bone marrow of a kitten showing pseudopodia extending into a blood vessel, *V*, and giving rise to blood platelets, *bp*. (After Wright.)

The process of the formation of red blood corpuscles is called *hæmopoiesis*. Before birth it is accomplished in the yolk sac and mesenchymatous tissues, and also in the liver and spleen. In later life, and particularly in mammals, hæmopoietic tissue is mostly confined to bone marrow, where *giant erythroblast cells* maintain the incessant production of new erythrocytes (Fig. 267).

4. Leucocytes

Intermingled with the red corpuscles in the blood are "white blood cells," or *leucocytes* (Fig. 268). Unlike erythrocytes of mammals these are detached cells that not only retain their nuclei throughout life, but possess other characteristic features of true cells. Within the same organisms leucocytes show considerable differences with respect to the character of their nuclei, general size and shape, differences that make possible their classification into three general kinds, namely, lymphocytes, granulocytes, and monocytes. It should be noted that this classification is based upon the leucocytes of human blood which have been most studied.

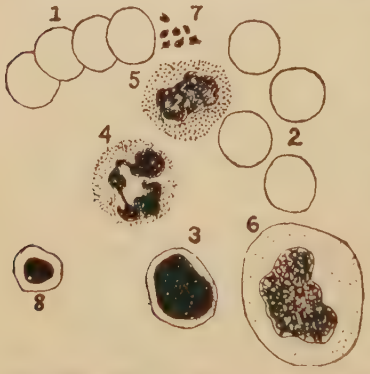


FIG. 268.—Blood cells. *1*, red blood corpuscles in *rouleau* formation; *2*, red blood corpuscles, surface view; *3*, lymphocyte; *4*, polymorphonuclear leucocyte; *5*, basophil leucocyte; *6*, large mononuclear leucocyte; *7*, blood platelets; *8*, nucleated erythrocyte. (After Jordan and Ferguson.)

Lymphocytes constitute normally something like twenty-two to twenty-five per cent of all leucocytes. They are roughly spherical, with a single nucleus, and are smaller than erythrocytes, being from four to seven micra in diameter.

Granulocytes, which are somewhat larger than lymphocytes, being from seven to ten micra in diameter, are characteristically ameboid in shape and behavior. They are often referred to as "polymorphonuclear leucocytes" from the fact that their nuclei generally assume a variety of shapes. The granular cytoplasm, which gives the name "granulocyte" to these cells, has differential staining properties that, according to Ehrlich, serve to classify them still further, into *neutrophils*, *eosinophils*, and *basophils*. The two latter kinds are comparatively rare, forming only about three per cent and five tenths per cent respectively of the total number of leucocytes, while neutrophils furnish in the neighborhood of seventy per cent. As these percentages vary to a considerable extent pathologically, they make an extremely valuable indicator of abnormal conditions to the clinician.

Monocytes are giant mononuclear leucocytes, twenty micra or more in diameter, constituting normally from two to ten per cent of all leucocytes.

Dana and Carlson have pointed out that the number of new leucocytes contributed daily to the blood stream may be greater than the total number present in the blood. In man the total number of leucocytes of all kinds varies from 2,000 to 13,000 per cubic millimeter, with a normal average around 4,000. The range of numerical variation is proportionately much greater than that of erythrocytes. There is a normal increase in the number of leucocytes, for instance, after eating or vigorous exercise, upon exposure to cold, and during pregnancy. When the number rises to over 10,000, it indicates a pathological condition.

With regard to their *origin*, different kinds of leucocytes may be produced, like erythrocytes, in different parts of the body. In mammals certain cells, *myelocytes*, within the bone marrow, that do not circulate, are no doubt the busiest factories for the manufacture of white, as well as red blood cells, while embryonic mesenchyme is also another source of origin for both kinds of blood cells. With regard to their *renewal*, however, leucocytes, unlike erythrocytes, have the power of increasing in number by fission wherever they collect in lymphoid tissue throughout the body. Such foci are called *lymph nodes* and *lymph glands*.

The three kinds of leucocytes accomplish a variety of functions. For example, the wandering granulocytes, as well as monocytes, remove worn-out tissue cells and invading bacteria by engulfing and digesting them in true ameboid fashion, when they are known as *phagocytes;* the lymphocytes in the lacteals, or lymphatic vessels that enmesh the intestine, transfer fat globules, emulsified in their cytoplasm; while the giant monocytes have other though less known functions.

The granulocytes, with their ameboid pseudopods, are able to creep against the blood stream when necessary along the inner walls of blood vessels, with an independent movement of their own, and are frequently found more numerous in the peripheral region of the channel within the blood vessels than in the middle of the stream where erythrocytes are being passively floated along. Owing to their power of assuming a variety of shapes they are even able to squeeze between the irregular margins of the flat

endothelial cells forming the walls of the capillaries, (Fig. 269) thus escaping entirely from the blood vessels into the interstices between the cells of tissues, in their phagocytic forays. Indeed there is hardly a nook or cranny in the body that cannot be sought out and penetrated by these nomadic benefactors in the course of their sanitary and curative peregrinations. This escape through the capillary walls of phagocytes, or cell-devouring granulocytes, is termed *diapedesis*, and by its means some of the more important functions of the blood are accomplished. Once escaped, however, phagocytes must be returned to the blood stream, and this is accomplished by the lymphatic vessels. Meantime, the endothelial cells of the capillary walls immediately repair their walls after being thus broken through, so that erythrocytes are kept within bounds.

FIG. 269.—Diapedesis of leucocytes. (After Burton-Opitz.)

5. Thrombocytes

In addition to erythrocytes and leucocytes there are present in vertebrate blood other less well-known bodies, generally called *thrombocytes*. In the blood of the frog these have been described as "spindle cells" (Fig. 266), which are intermediate in character between the red and white blood cells, and are perhaps able upon occasion to transform into either. Their unstable character is shown by the fact that they tend to mass together and dissolve as soon as blood is shed, which makes careful detailed observation of them difficult. Although true spindle cells have been found in certain fishes, amphibians, reptiles, and birds, they are not present in mammals. Their place in mammalian blood seems to be taken by small bodies which Bizzozero has named "blood platelets" (Fig. 268).

The term "thrombocyte" (*thrombus*, clot; *cyte*, cell) is not a very happy one to apply to blood platelets because these are not true cells at all, but probably small, non-nucleated fragments of cells, with slight ameboid motility. They do, however, have to do with forming the "thrombus," or clot, which prevents excessive hemorrhage in case of wounds.

The various kinds of thrombocytes vary in size from five-tenths

to four micra in diameter in man, thus being always considerably smaller than erythrocytes. In number they have been estimated to be from 200,000 to 778,000 per cubic millimeter, with 500,000 given by Howell for human blood. According to Wright, blood platelets have their origin in the giant erythroblast cells of bone marrow, from which they are constricted off.

When withdrawn from blood vessels and exposed to air, blood platelets quickly change from rounded bodies into spindle and star-like shapes, and then disintegrate, making a prolonged technical study of them difficult.

6. Plasma

Two-thirds of blood is fluid *plasma*, which in turn is 80 per cent water. The plasma is a non-living fluid of probably more chemical complexity within the body than appears in the test tube. It contains a constantly changing variety of substances in solution, chief among which are dissolved *food materials* on the way to cellular delivery, and *waste products* that are being collected for elimination. There are also present *enzymes* of various sorts which activate chemical changes; *opsonins*, that prepare trespassing bacteria for phagocytosis; *hormones*, the chemical messengers from endocrine glands on their way to the performance of tasks of internal regulation; *antitoxins*, *complement*, *amboceptors*, and various other problematical substances engaged in constant warfare against harmful invasion; finally, there is *fibrinogen*, which plays an important rôle in the clotting of blood.

If it were not for the mechanism of the blood clot, loss of blood from wounds which open the blood vessels would prove to be much more serious than it is. According to Howell, a substance known as *prothrombin* is produced by the blood platelets when they disintegrate upon exposure to the air. Prothrombin in the presence of *calcium salts* in the blood forms *thrombin*, and this precipitates the fibrinogen in the blood to form a *fibrin mesh* in which blood cells become entangled, making a clot. The clot thus formed acts as an emergency plug to prevent the escape of blood while organic repairs are being made.

A blood clot that breaks free and circulates within the blood vessels until it meets obstruction, is termed an *embolus*. Such a blood clot caught in the capillaries of the brain may give rise to a "shock," or apoplexy, recovery from which is dependent upon the removal of the embolus by absorption or other means.

III. BLOOD CHANNELS

1. The Evolution of Organic Irrigation

Blood channels may be looked upon as equivalent to the outer surface of the body, or as devices for increasing the surface area of the organism which is exposable to a nutritive and respiratory environment. In most invertebrates blood channels are largely lacunar or perivisceral spaces. The first evolutionary stages in the development of a circulatory apparatus are to be seen in the porous sponges, whose "blood," i.e., the surrounding water, carries a random charge of food and air past the loosely organized colonial cells of the sponge body. In flatworms and some medusæ also, there are neither true blood channels nor any specialized food-carrying medium of blood, because in these lowly creatures the digestive tube itself branches out like the twigs of a tree, extending in between all the cells of the body in such a way as to effect a direct delivery of needful nutrition.

Among vertebrates two general types of channels appear, namely, a *hæmal system* of closed tubes carrying blood, and an auxiliary *lymphatic system* carrying lymph.

In general, blood channels form a system of irrigation consisting of a continuous series of cavities, lined throughout with flat endothelial cells, in which the blood circulates. The fact that blood is not subject to ebb and flow but is constantly in motion, and that it repeatedly makes the entire circuit of the blood vessels during life, was established in 1619 by William Harvey (1578–1657), long before anyone actually saw the blood pass through the smaller connective channels. In 1696 Leeuwenhoek described the capillary circulation in a bat's wing, as follows:

> "I perceived in many places, an artery and a vein placed close beside each other and of a size large enough to admit the passage of ten or twelve globules at the same time; and in this artery the blood was protruded or driven forward with great swiftness, and flowed back through the vein, which was a most pleasing spectacle to behold."

Although the circulatory system penetrates to nearly every part of the living organism, there are a few regions of the highly differentiated vertebrate body that are not invaded by blood vessels of any kind, namely, the cornea of the eye, cartilage tissue, and the epidermis together with its derivatives, the hair, nails, feathers, horns, and claws.

2. General Plans of Circulation

Blood vessels are related to each other in the following order:

Arteries
Arterioles
Arterial capillaries
HEART — Capillaries
Venous capillaries
Venules
Veins

Four general plans may be indicated, viz., annelid, amphioxus, fish, mammal.

A. ANNELID PLAN

Two longitudinal blood vessels, one dorsal and one ventral, connected at either end by capillary networks, make up the cir-

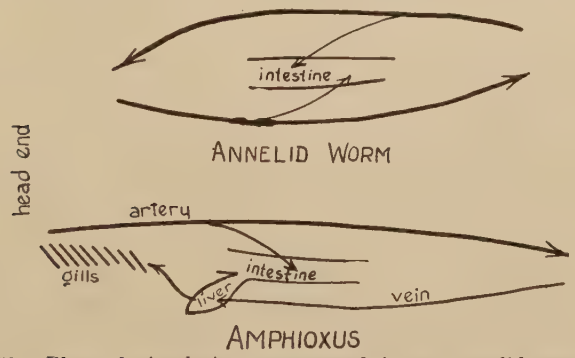


FIG. 270.—Plan of circulation, contrasted in an annelid worm and amphioxus.

culatory system of the practically heartless annelids. The blood flows forward along the dorsal vessel and backward through the ventral vessel in the simplest manner (Fig. 270).

B. AMPHIOXUS PLAN

Amphioxus, the lowest vertebrate, bears a general resemblance to the invertebrate annelids in its circulatory system which has, however, two notable differences. First, the blood flows around, in the opposite direction from that of the annelid plan, and second, there is introduced along the course of the ventral vessel, before even the semblance of a heart appears, an extra capillary network

that spreads over the diverticulum of the gut (the ancestral liver), forming a primitive *hepatic portal system* (Fig. 270). Moreover, in common with other lower vertebrates, a large part of its anterior capillary system passes through the gills, which extend along half the digestive tube. Most of the posterior capillaries enwrap the remainder of the digestive tube together with its liver diverticulum. Thus, the two major functions of the blood, namely, respiration and nutrition, are localized by the arrangement of the capillaries.

C. Gill Plan of Fishes

The amphioxus plan becomes further elaborated in fishes (Fig. 271), by the development of a *heart*, and the introduction of an

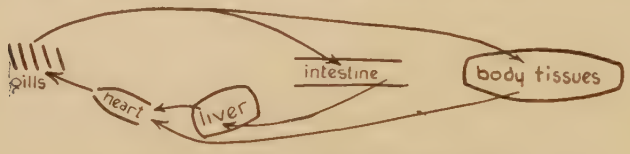


Fig. 271.—Plan of circulation in a fish.

additional capillary complex involving the kidneys, called the *renal portal system.*

The heart is simply an enlargement and modification of a part of the main ventral blood vessel lying between the hepatic portal capillaries and the gills, whereby the tube becomes constricted into four tandem chambers through which the blood flows forward.

The renal portal system (Fig. 280, A) is a special device for the return of blood from the region of the large propeller-like tail, characteristic of fishes, through a capillary network in the kidneys, thence joining the main blood stream secondarily. It is not shown in Fig. 271. In fishes, therefore, besides the capillaries which unite the outward distributing system of blood vessels (arteries) with the inward collecting system (veins) there are two notable strainer-like complexes of capillaries, or portal systems, within the kidneys and liver respectively, that interrupt the stream of blood returning to the heart.

D. Lung Plan of Mammals

The general plan of the circulation among higher vertebrates when reduced to the simplest terms, may be represented by the diagram in Fig. 272. The dotted line, which is connected at only one end with the circulatory system, stands for the auxil-

iary lymphatic system. This collects lymph that has escaped from the capillaries from all regions of the body, returning it to the venous system just before it reaches the heart.

It will be seen that the methods of respiration and locomotion both have to do with modifying the circulatory plan.

The change from branchial respiration by means of gills to pulmonary respiration through lungs, makes necessary a double blood circuit instead of a single one, as in fishes, with two central clearing houses, or hearts, which are placed so intimately together that, looked at superficially, they have the appearance of one,

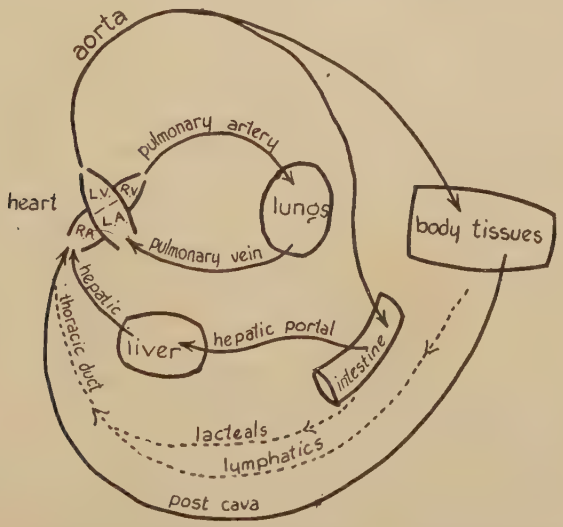


FIG. 272.—The plan of circulation in a mammal. *L.A.*, left auricle; *L.V.*, left ventricle; *R.A.*, right auricle; *R.V.*, right ventricle.

while the renal portal system becomes discontinued with the diminishing importance of the tail and the evolution of locomotion on land by means of legs.

3. Structure of Blood Vessels

The walls of blood vessels show certain differences that serve to distinguish arteries, veins, capillaries, and lymphatics from each other. Arteries and veins of the same size are not to be confused since veins have thinner walls and a larger cavity within, and consequently are more liable to collapse when emptied of blood.

Both arteries and veins present three layers of tissue (Fig. 273), known as tunica intima, tunica media, and tunica adventitia. The inside layer, or *tunica intima*, is invariably made up of a lining of flat endothelium, continuous and universal in all blood vessels including the heart itself, and wrapped about by reinforcing connective tissue and elastic fibers. The middle layer, or *tunica media*, is largely smooth muscle cells, mostly arranged in circular fashion and interspersed with connective and elastic tissue; while the outer layer, or *tunica adventitia*, is principally connective and elastic tissue, penetrated by lymphatics, and vasomotor nerve fibers, which control the changing calibre of the blood vessel. Certain veins in man, such as the umbilical, iliac, splenic, renal, and superior mesenteric, are noteworthy because longitudinal muscle fibers also are found in their outside layer.

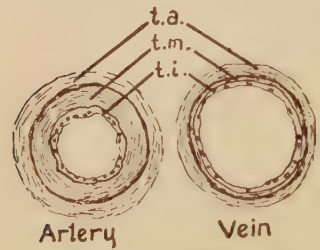


FIG. 273.—Transverse section of an artery and a vein of corresponding size, showing the three layers; *t.a.*, tunica adventitia; *t.m.*, tunica media; and *t.i.*, tunica intima. (After Huxley.)

Arteries are thick-walled conduits carrying blood away from the heart, which are characterized by a well-developed contractile tunica media, that maintains the shape of the blood vessel without collapse, and a relatively thin tunica adventitia. As they follow their course throughout the body they decrease in size, passing over into arterioles, arterial capillaries, and eventually true capillaries. These form innumerable anastomoses between the arterial capillaries on the one side and the venous capillaries on the other. True capillaries lack both tunica media and tunica adventitia, having for a wall only the single innermost layer of flat endothelial cells from the tunica intima. Arterial and venous capillaries, therefore, are transitional in size and thickness between the capillaries proper and the arterioles and venules respectively.

Veins, which always *begin* with capillaries, are relatively thin-walled and collapsible. Since their walls are deficient in the elastic tissue and muscle cells of the tunica media, the tunica adventitia becomes the most highly developed of their three layers.

Valves, which hinder or prevent the backsetting of the blood (Fig. 274), are present in many veins but not in arteries, except in the immediate neighborhood of the heart of some gill-breathers.

Valves are absent from the veins of the brain, cord, meninges, bone, and the umbilical vein, as well as most visceral veins, except branches of the hepatic portal system. The thin-walled veins are much more likely to anastomose, become varicose, or to enlarge into sinuses, than the thick-walled arteries.

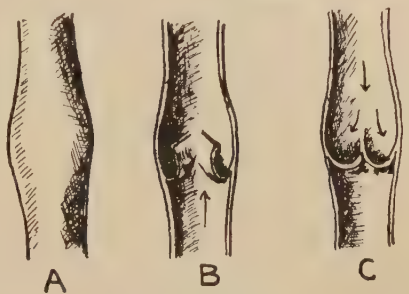


FIG. 274.—Valves in veins. *A*, swollen vein from the outside indicating the presence of a valve; *B*, valve open allowing the blood to flow in the direction of the arrow; *C*, valve closed preventing the flow of blood in the direction of the arrows.

Lymphatics are typically varicose as well as capable of great distension. Ordinarily they do not acquire thick muscular or elastic walls and are very collapsible, although the larger lymphatics develop a definite tunica media with muscle cells, and may even pulsate. They entwine around other blood vessels in the most intimate fashion, yet do not communicate with them except at one or two definite places near the heart. Lymph capillaries, although never so small as hæmal capillaries, have the same sort of thin endothelial walls.

Physiologically, if not morphologically, the large serous cavities, such as the body cavity, and the pericardial and pleural cavities, as well as the synovial spaces around joints, belong to the lymphatic system, although their walls have a somewhat different origin and structure from those of ordinary lymphatic vessels.

Lymphatics, like veins, possess valves along their course, which are crescentic folds of the tunica intima, preventing to any great extent the retreat of the fluid away from the heart.

4. The Rôle of the Capillaries

The first blood vessels to form embryologically are *capillaries* (*capilla*, little hair). Physiologically they are the most important part of the intricate system of blood channels in the vertebrate body, because it is in them that the final business of the circulatory system is accomplished.

As has been said, both arteries and veins have their origin in capillaries, extending from their source by terminal growth. If the entire circulatory system be compared to a railroad system,

capillaries correspond to stations where passengers and freight are entrained and detrained, while the more conspicuous arteries and veins are simply lines of track connecting the stations.

Anatomists have always been more concerned with tracing and homologizing veins and arteries which it is possible to identify, than with capillaries, that, by reason of their complexity and numbers, defy cataloguing. When one considers Krogh's estimate, that there may be at least 2,000 different capillaries in a square millimeter of human muscle, and that the total length of the capillaries of the body, if placed end to end, would be as much as 100,000 kilometers, or two and one-half times around the earth, it is small wonder that anatomists are forced to describe them in the most general terms. Unlike the twigs of a tree they

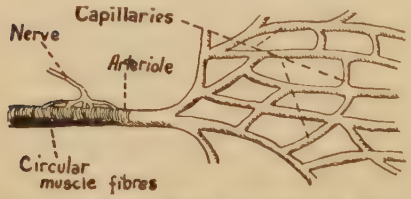


FIG. 275. — A terminal arteriole, surrounded by a "stop-cock" cuff of circular muscle fibers, which is supplied by a nerve ending for regulating the flow of the blood. The capillary network having greater internal expanse than the arteriole shows why the blood flows more slowly through the capillaries than in the arterioles. (After Keith.)

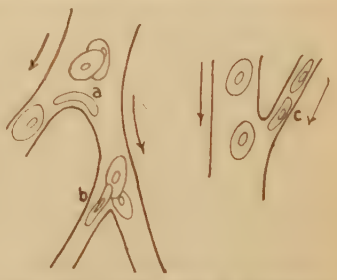


FIG. 276. — Diagram to illustrate the behavior of red blood corpuscles in the capillaries. The arrows mark the course of the blood. *a*, a "saddlebag" corpuscle; *b*, corpuscle bending itself as it enters a side branch; *c*, deformity in a narrow capillary. (After Howell.)

extend *without diminution in calibre*, as a result of which there is usually more total internal passage-way in the anastomosing network of capillaries than in the larger blood vessels which they immediately connect (Fig. 275). In places they are so small that the blood corpuscles have to change shape in order to squeeze through in single file (Fig. 276).

Sometimes they abruptly interrupt the course of venules or arterioles and form special networks, called *retia mirabilia*. Such networks are found in the chorioid layer of the eyeball; in the "pseudobranchs" on the walls of the spiracular clefts in elasmobranchs; in the "red gland" within the swim bladder of fishes; and in the glomeruli of kidneys. Capillaries are generally inter-

mediaries between veins and arteries, but they may connect veins and veins, when they constitute a "portal system," or arteries and arteries, as in the gills of fishes.

5. Arteries and Their Transformations

Arteries, as already indicated, are blood vessels leading, in the physiological sense, away from the heart and ending in capillaries. The course which the arteries follow in their task of distributing a proper blood supply throughout the body, is best understood by considering it as divided into posterior and anterior sections with reference to the location of the heart. Of the two sections the posterior one is much the simpler with reference to the modifications that it undergoes in the vertebrate series, and it will be unnecessary to consider it in detail. The anterior arteries, however, that bear the brunt of the transformation from water to land life, require some description.

In fishes one main trunk line (Fig. 277, B), the *ventral aorta*, leaves the heart and passes forward, embedded in muscles and connective tissue. It soon branches on either side into paired *afferent branchial arteries* which go to the gills, there losing their identity in a maze of capillaries, only to emerge on the dorsal side as paired *efferent branchial arteries*, which unite to form a large single *dorsal aorta*. From the main trunk line of this dorsal aorta, branches are given off that supply all the organs and regions of the body.

In the higher vertebrates which have lost their gills and acquired a double heart, the dorsal aorta arises from the heart on the left side, and without suffering any interruption of gill capillaries, proceeds directly, after making a horseshoe loop, to supply all parts of the body. Meanwhile another arterial trunk line, the *pulmonary artery*, leaves the heart on the right side to deliver blood to the lungs.

In the entire vertebrate series the fate of all the arteries that arise from the dorsal aorta, when once it loops around to pass backward within the body cavity, is much the same, in that all organs and regions of the body receive branches of adequate size in due order. Therefore the comparative anatomist does not have important differences to record in the various classes of vertebrates. The more significant transformations of the arterial system are centered about the gill arches and their remains. An examination of this part of the arterial system in different vertebrates is, therefore, profitable.

In amphioxus the ventral aorta is connected with the dorsal aorta by a number of pairs of lateral branchial loops that encircle

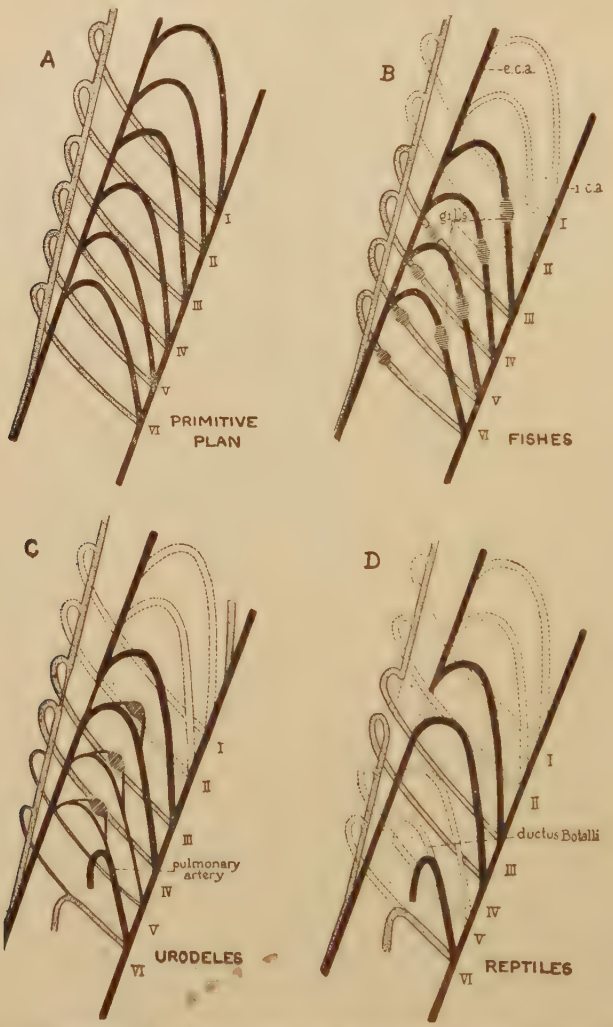


FIG. 277.—Diagrams of the arrangement of the arterial loops in various vertebrates. *A*, primitive theoretical plan; *B*, teleosts; *C*, urodeles; *D*, reptiles. *I*, mandibular arch; *II*, hyoid arch; *III-VI*, branchial arches; *e.c.a.*, external carotid artery; *i.c.a.*, internal carotid artery. See also Fig. 279.

the anterior part of the digestive tube and supply the gill capillaries. These loops increase in number with age and may become

as many as sixty pairs in the adult animal, occupying a large portion of the anterior region of the body.

In other vertebrates the number of pairs of branchial loops present during embryonic development, is typically six,[1] although much modification occurs in different vertebrates.

The primitive embryonic arrangement of these arterial vessels is indicated in Fig. 277, A. It will be seen that the loops do not connect directly with the dorsal aorta, but with two smaller blood vessels, the *radices aortæ*, which secondarily join in the form of the letter Y, to make the dorsal aorta.

The fate in the vertebrate series of these six pairs of embryonic loops, gives one the essential modifications in the comparative anatomy of the arterial system, for, as already mentioned, the distribution of the blood supply from the trunk line of the dorsal aorta over the body does not present fundamental differences in the various vertebrate classes.

In teleost fishes (Fig. 277, B), the two most anterior pairs of loops, namely, the mandibular (I) and the hyoid (II), are suppressed in adult life, while the remaining four (III, IV, V, VI) become the branchial arches, interrupted by gill capillaries. The anterior prolongations of the ventral aorta become the *internal carotid arteries*, and a similar extension of the radicæ aortæ, the *external carotid arteries*. These arteries supply the head region.

Passing to the Amphibia the plan of the arterial arches in the gill-breathing urodeles (Fig. 277, C) may be understood when it is projected against the background of the primitive embryonic type. The *external gills* of amphibians, unlike the *internal gills* of fishes, do not directly interrupt the branchial loops, but are established on a detour, so that it is possible for the blood to pass from the ventral to the dorsal aorta by two routes, one through the uninterrupted branchial loop, and the other by the way of a side line through the capillaries of the external gills. Three pairs of such external gills may be present in urodeles, on loops IV, V, and VI. Thus it is possible in those salamanders that discard their gills during metamorphosis, for the blood to continue without interruption by way of the branchial loops direct, avoiding the disastrous consequences which would inevitably result in the single internal gill route of fishes, if it should be put out of commission.

[1] Certain primitive sharks, for example, *Hexanchus*, have seven, and some cyclostomes exceed the typical number.

In urodeles, it should be noted, the last posterior loop (VI) becomes for the most part diverted as the pulmonary artery, to go to the lungs instead of to the dorsal aorta, while the radicæ aortæ between loops III and IV become much attenuated.

The anuran amphibians, exemplified by the frog (Fig. 278), pass through a tadpole stage in which their arteries resemble

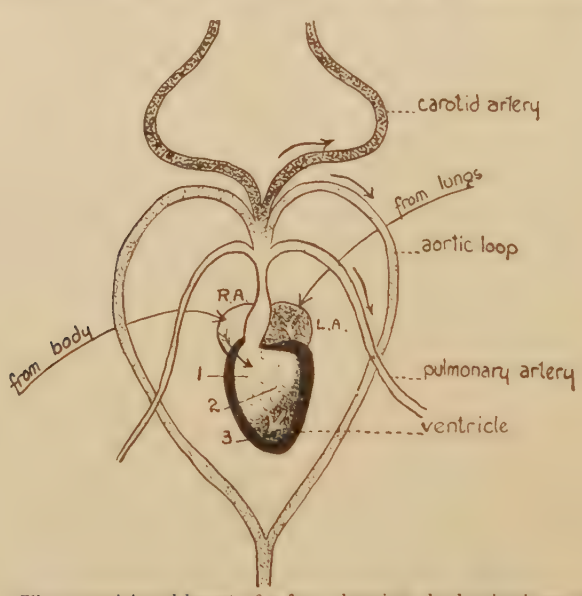


FIG. 278.—The transitional heart of a frog showing the beginnings of differential distribution of blood with a single ventricle. *L.A.*, left auricle; *R.A.*, right auricle. The aërated blood from the lungs is emptied into the bottom of the ventricle from the left auricle, and the non-aërated blood from over the body enters the upper part of the ventricle from the right auricle. Both of these contributions are pumped out before there is opportunity for much mixture, so that three kinds of blood, non-aërated, mixed, and aërated, are sent out of the contracting ventricle in the order 1, 2, 3. The non-aërated blood, *1*, takes the first accessible avenue of escape through the pulmonary arteries to the lungs; the mixed blood, *2*, fills the second possible available channel, the aortic loop, going over the body; while the aërated blood, *3*, from the bottom of the heart goes to the head through the carotid arteries since the other passages are already crowded full.

those of the urodeles, but go a step further in discarding ancestral arterial pathways, since only three pairs (III, IV, and VI) of the six embryonic loops, survive in the adult. Loop IV becomes the large *aortic arch*, while loop III is entirely devoted to supplying the head region, as the connectives between III and IV on the radices aortæ disappear, so that blood in the third loop can no

longer pass directly into the dorsal aorta. That part of loop VI which does not go into the formation of the pulmonary artery is reduced to a stretch of "dead track," named the *ductus arteriosus* ("ductus Botalli"), through which no blood passes. Loop V, that showed signs of degeneration in the perennibranchiate urodeles, disappears entirely in the adult frog.

The same three pairs of loops survive in the reptiles (Fig. 277, D). There is, however, one distinct difference with regard to the aortic arch (IV). This arch on its left side becomes split off from the rest of the ventral aorta, and carries a different quality of

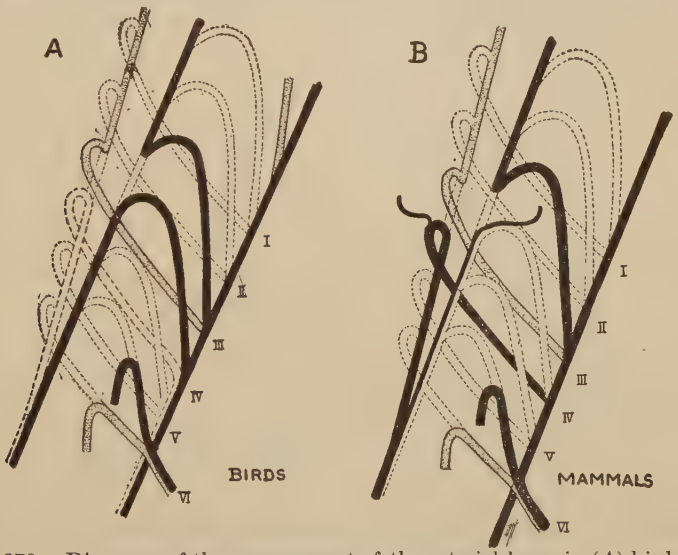


FIG. 279.—Diagrams of the arrangement of the arterial loops in (*A*) birds and (*B*) mammals. (Lettering as in Fig. 277.)

blood to the dorsal aorta from that borne in the right side, since it connects with a newly established chamber of the heart. In amphibians the mixture of aërated and non-aërated blood occurs in the heart before it is sent over the body, but in reptiles, which have more complete partitions established between the chambers of the heart, the mixing of "pure" with "impure" blood is postponed until the right and left branches of loop IV pour their diverse contributions into the dorsal aorta. Reptiles as well as amphibians, however, are "cold-blooded."

Birds (Fig. 279, A) and mammals (Fig. 279, B), show a still greater reduction of arterial byways, since in each case one-half

of the pair of aortic loops is suppressed. The right half remains in birds, the left half in mammals.

The single large aortic loop that arises from the heart in man, arches over to the left and passes downward to supply the body and its various organs, thus becoming the transformed product of the embryonic ventral aorta, the left side of the fourth branchial loop, and the dorsal aorta.

Occasional rare cases reported in medical literature of double aortic arches in man, find a ready interpretation in the light of comparative anatomy. In man too there is a single ductus Botalli on the left side as a part of the sixth embryonic loop, and this remains open for the passage of blood during uterine life, until at birth pulmonary respiration is established.

6. Evolution of the Venous Routes

The channels by means of which the blood is collected and returned to the heart have undergone a greater degree of evolutionary adaptation in the vertebrate series, than the corresponding arteries that distribute the blood from the heart over the body. This is due in part to the elaborate complexes of capillaries inserted in the course of the veins, which form the "portal" systems, and in part to the accessory services of the lymphatic system of channels.

As would be expected the least complicated arrangement of veins is found in amphioxus. An unpaired caudal vein picks up blood from the postanal region of the body and, making a loop around the anus, continues forward beneath the intestine as the *subintestinal vein*, receiving contributions from the capillaries that encircle the alimentary canal, and deriving food therefrom. Near its anterior end the subintestinal vein breaks up into a primitive hepatic portal system as it reaches the liver diverticulum, while a blood vessel, out of which the heart and ventral aorta are destined to evolve later in the fishes, goes forward from the liver to the gills.

The venous system of an elasmobranch is diagrammatically represented in Fig. 280, A. It will be seen that the heart not only receives blood that has been strained through the liver from the *hepatic veins* of the hepatic portal system, but that there are also on either side *anterior cardinal* and *inferior jugular veins* bringing back blood from the dorsal and ventral regions respectively, of the head, while *postcardinal* and *lateral veins* do a similar service for the body in general. All these veins converge to form

on either side a common channel, the *duct of Cuvier*, that opens directly into the heart. The *subclavian veins* from the pectoral fins, or "arms," empty also near this point of convergence. The

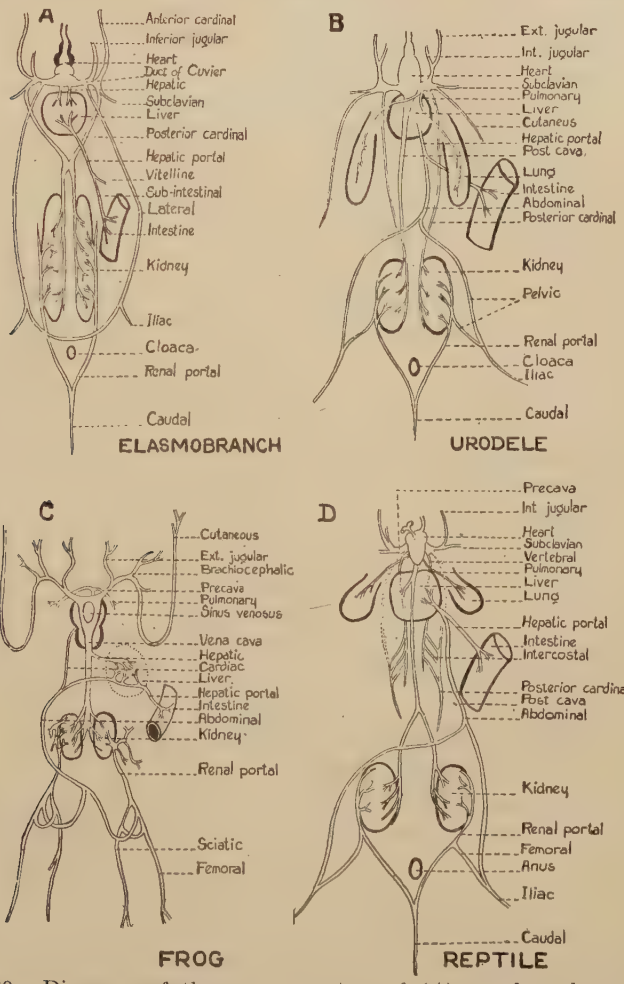


FIG. 280.—Diagrams of the venous system of (*A*) an elasmobranch; (*B*) urodele; (*C*) frog; and (*D*) reptile.

iliac veins from the pelvic fins, or posterior paired appendages, are contributory branches to the lateral veins which run along the body wall, either to empty independently into the ducts of Cuvier or indirectly after joining the postcardinals.

The *caudal vein*, ordinarily draining a large area in the fishes, forks like a letter Y at the anus and sends a diminishing branch along the outer margin of each elongated kidney. These branches subdivide until they become capillaries within the kidneys, emerging eventually into the postcardinals, thus forming the *renal portal system.*

It will be seen that there are, therefore, three venous systems combined in the elasmobranch fishes, namely, the *cardinal system*, including tributaries draining the head and body wall with various organs in the body cavity; the *hepatic portal system*, from the digestive tube; and the *renal portal system*, from the large tail region and the kidneys.

In many elasmobranch fishes also there is still to be seen along the ventral wall of the digestive tube in intimate relation with the spiral valve within, a *subintestinal vein* like that of amphioxus. This is the anterior continuation of the caudal vein, but instead of forming the main trunk line and passing directly to the liver to form the hepatic portal network, as in amphioxus, it empties first, during embryonic life, into one of the two large temporary *vitelline veins* that bring the blood from the yolk sac. In the higher vertebrates the *omphalomesenteric veins*, thus formed by the union of the intestinal and the vitelline components, break up to form the hepatic portal complex within the liver.

In the larger group of bony fishes (teleosts) the venous arrangement is much like that of the cartilaginous elasmobranchs, except that the lateral veins disappear, and the traffic from the body wall and pelvic fins, formerly handled by the lateral veins, is taken over by the postcardinals.

Salamanders and frogs, as representative amphibians, present two further stages in the evolution of the veins of vertebrates which can be understood by comparison with the more primitive arrangement already described in elasmobranch fishes. The plan of the principal veins in salamanders, as shown diagrammatically in Fig. 280, B, presents three striking innovations. First, the appearance of a new vein should be noted, the *postcava*, which rivals the postcardinals in collecting blood from the posterior part of the body. This important blood channel fuses with the right postcardinal in the region near the kidneys, and extends forward through the liver to the heart, as a single vein. Although like the subintestinal vein of amphioxus and the cyclo-

stomes in this respect, it is not homologous with that vein, being dorsal to the intestine and lying close to the aorta along the body wall, while the subintestinal vein is ventral to the intestine and quite independent of the body wall.

Secondly, the iliac veins, instead of opening into the lateral veins as in elasmobranchs, fork on either side, sending one branch to the renal portal system at the kidneys, while the other branch, which is homologous with the lateral veins of the elasmobranchs, unites with its fellow on the other side to form a median *abdominal vein* that empties anteriorly into the hepatic portal system. Blood returning from the hind legs of an amphibian, therefore, must pass through either the renal portal, or the hepatic portal strainer before reaching the heart, whereas in fishes the iliac blood goes direct to the heart by way of the lateral veins without portal interference of any kind.

Thirdly, amphibians, since they use the skin to a considerable extent as a supplementary breathing organ, have in addition to *pulmonary veins* from the lungs, a pair of well developed *cutaneous veins*. Diagrammatically these bear a superficial resemblance to the lateral veins of elasmobranchs but should not be confused with them.

The arrangement of the veins in the frog embryo, or "tadpole," is like that of a salamander, except that the rivalry between the newly established postcava and the diminishing postcardinals, culminates in the successful monopoly of the circulatory blood traffic by the former and the disappearance of the latter (Fig. 280, C). With the elimination of the postcardinals, the anterior cardinals become continuous with the ducts of Cuvier, forming the *precavas*, which in turn are continuous with the *jugular veins* that now return blood from the head directly into the right auricle of the heart.

Moreover, with the loss of the tail the caudal vein vanishes, and in consequence the "portal," or carrying, part of the renal portal system, is transferred entirely to the iliac veins. Such drastic changes as these, designed to meet the difficult conditions accompanying the precarious transitional method of their life, are typical of the bodily makeshifts which this small struggling group of vertebrates has had to resort to in order to accomplish the great evolutionary feat of emerging from water to land.

As a matter of convenience, reptiles and birds have been put

together by Huxley and called the *Sauropsida*, since they have many anatomical features in common which distinguish them from fishes and amphibians (*Ichthyopsida*) on the one hand and *mammals* on the other.

While both the sauropsida and the mammals are based on the preceding plan of the ichthyopsida, they have undergone somewhat divergent modification with respect to the routes of the veins, so that the sauropsida represent more properly a side relationship to the mammals, like that of cousins rather than of ancestors in the direct line.

The anterior part of the postcardinal atrophies, and a pair of longitudinal *vertebral veins* (Fig. 280, D), formed out of anastomoses of branches of the *intersegmental veins*, come into prominence, annexing themselves to the anterior cardinals before emptying into the ducts of Cuvier. Posteriorly the vertebral veins connect with the remains of the disappearing postcardinal system through the transverse *intercostal veins*.

The renal portal system, the fate of which is intimately bound up with the mesonephric excretory apparatus, although persisting in reptiles, becomes extremely reduced in birds, and disappears entirely in mammals, along with the replacement of the mesonephric system by the metanephric plan of excretory organs, that is, the "permanent kidneys."

The abdominal vein of amphibians and reptiles, comparable to the lateral veins of fishes, merges into an *epigastric vein* in birds (Fig. 281, A), which is possibly homologous with the *umbilical vein* of mammals.

In lizards, snakes and turtles, as pointed out by H. L. Bruner,[1] the venous system in the head region is characterized by an abundance of *sinuses*, or blood-filled enlargements of the veins, both inside and outside of the cranium. These modifications of the head veins are much less in evidence in the Crocodilia than in the three lower groups of reptiles just mentioned. Through a modification of the blood pressure in the superficial sinuses that extend outside of the skull beneath the skin, the molting (ecdysis) of the corneal layer is accomplished. Recourse to some such device is necessary in the case of these reptiles because they are enveloped in thick dry scaly skins which do not easily allow for the necessary periodical casting off of the dead, inelastic outside part of the integument.

[1] *Amer. Jour. Anat.*, Vol. VII, 1907.

In *Phrynosoma*, the "horned toad" of the cactus regions of southwestern United States, the venous sinuses, together with associated muscles, form a curious mechanism whereby these grotesque animals, under excitement, are able to squirt blood from their eyes.

Among mammals (Fig. 281, B), the persisting anterior ends of the postcardinals, together with the *supracardinals* which are formed in their neighborhood, become the *azygos system*. The

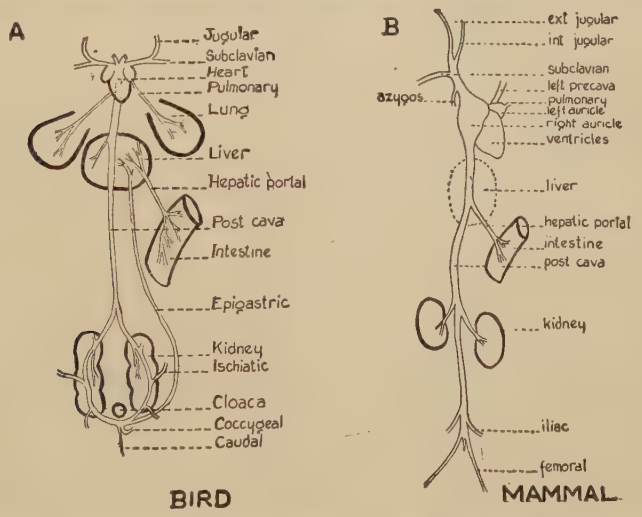


FIG. 281.—Diagrams of the venous system of (*A*) a bird and (*B*) a mammal.

stub of the right postcardinal, with the supracardinal on the same side, forms the *azygos vein*, while a fragment of the left postcardinal and the left supracardinal, join as the *hemiazygos vein*, which is connected by anastomosing bridges to the azygos vein.

In marsupials, rodents, insectivores, and many artiodactyls, the azygos system is about equally developed on the two sides, while in the head region two precavas, in balanced fashion, return blood to the heart. In carnivores, edentates, and primates, on the other hand, a reduction of the left azygos system results in an asymmetrical shifting of most of the blood of this area to the right side for delivery to the heart, while in the head region the right precava becomes dominant and the left precava degenerates into a pensioner in the form of the insignificant *oblique vein of the left atrium*. The blood on the left side of the head is now

delivered to the right side through the *left innominate vein* which connects the two jugular veins as the left precava atrophies.

Out of the remains of the left precava and the duct of Cuvier from which it arose, there persists the *great cardiac vein* which returns blood from the walls of the heart itself to the right auricle. Not only the heart but all of the larger blood vessels, arteries, veins, and lymphatics, are supplied in their outer walls (tunica adventitia) with a ramifying system of nutrient blood vessels, called *vasa vasorum*, or "vessels of the vessels," for, just as "shoemaker's children must have shoes," so the blood vessels themselves need to be provided with a circulatory mechanism for their own welfare.

There are also developed in the venous system of mammals a pair of *subcardinal veins*, parallel and ventral to the embryonic and ancestral postcardinals, which take part in the formation of the venous complex that drains the posterior part of the body.

7. Lymphatics

The lymphatic system, consisting of channels and spaces containing lymph, is anatomically and physiologically distinct from, but less conspicuous than, the more easily seen hæmal system of arteries, veins, and capillaries through which the blood courses.

A. Lymph

Lymph resembles blood in being a fluid containing detached cells, bearing the kaleidoscopic products of metabolism. It lacks respiratory red blood corpuscles, however, and blood platelets. All of its cellular elements are leucocytes, which having escaped by the process of *diapedesis* through the walls of the blood capillaries and after penetrating everywhere into the minute interstices of the tissues, are eventually rescued by the lymphatic vessels and returned to the red blood stream. Although lymph contains less fibrinogen than blood, it nevertheless retains the capacity to form a clot.

B. Lymph Channels

The lymphatic channels form an anastomosing network of conduits throughout the connective tissues of the body, in intimate association with arteries and veins which they probably equal if not exceed in total carrying capacity (Fig. 282). In size the lymphatic channels range from minute varicose capillaries to

large sinuses, or lymph reservoirs, such as the subcutaneous sacs under the skin of the frog (Fig. 283), which protect the delicate skin from excessive loss of moisture during the temporary excursions of this amphibian from water to land.

The body cavity of invertebrates contains lymphlike blood, and is an essential part of the lymphatic system that in the lower forms assumes primary importance over that of the red blood system from which it is not completely differentiated. In vertebrates the major cavities also, such as the peritoneal, pericardial, and pleural cavities, as well as the meningeal spaces about the nerve cord and brain, the synovial areas around joints, and the peri- and endolymphatic passage-ways of the inner ear, are all directly or indirectly a part of the lymphatic "underworld."

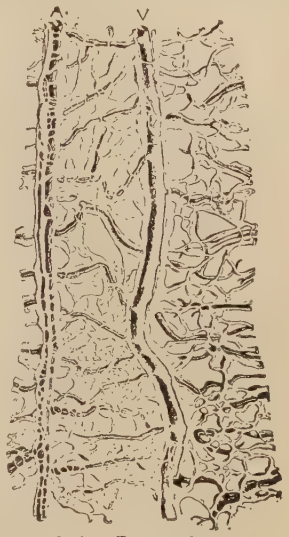


FIG. 282.—Lung of *Necturus* with the blood and lymph vessels injected. The lung was cut open, spread out flat, and mounted in balsam. *A*, artery; *V*, vein. Only the main branches of the artery and vein are shown. The blood and lymph vessels were drawn by means of the camera lucida and show the exact relations of both sets of vessels. (After Miller.)

Although the lymphatic channels are everywhere in most intimate contact with the blood vessels, they do not open directly into the blood system except at one or two definite places near the heart. The flow of the lymph is accomplished in some small degree by gravity, but its advance is principally brought about by muscular movements of the exercising body, by means of which it is squeezed along its one-way course towards the heart. Since the lymphatic channels

FIG. 283.—Subcutaneous lymph sacs of a frog. The skin is represented as removed and the sacs are outlined by lines of connective tissue that join the skin to the underlying muscles. (After Gaupp.)

are not connected with the red blood system at their distal ends, the pumping power of the heart can have no effect upon lymph movement, as it does upon the blood within the red blood system of channels of which the heart is an integral part. Unlike the blood, lymph always travels towards the heart, backsliding being prevented by valves which allow forward movement but prevent retreat. These valves are particularly noticeable in birds and mammals.

C. Lymph Hearts

In the lower vertebrates certain of the lymphatic vessels, which are near the junction of the lymphatic system with the veins, may acquire muscular walls and become pulsating *lymph hearts*, thus supplementing by their contraction the body muscles in affecting the movement of the lymph.

Among amphibians, cæcilians (Apoda) have a pair of pulsating lymph hearts for each of the numerous segments of their long wormlike bodies, while urodeles likewise possess a double row of several peripheral lymph hearts, situated along the posterior part of the lateral line on either side. Frogs, and other anurans, have typically four lymph hearts in adult life, placed, with reference to the four legs (Fig. 284), anteriorly at the level of the third vertebra near the junction of the subclavian vein with the jugular vein, and posteriorly at the base of the iliac veins on either side of the end of the urostyle.

Fig. 284.—Lymph hearts in a frog, *Rana*. *A*, antero-dorsal region; *B*, postero-ventral region. The lymph hearts are represented in black. (After Wiedersheim.)

In reptiles, only the posterior pair of lymph hearts typically persists, while in birds and mammals, even these vanish after a reminiscent embryonic appearance.

D. Thoracic Duct

The largest of the lymph vessels, into which all the others converge, opens into the venous system near the heart. This is the *subvertebral space* in fishes, which becomes a pair of *thoracic ducts* in reptiles, so called from their subvertebral position in the

thorax. In mammals, although embryologically paired, usually only the left thoracic duct persists, and this empties into the *left brachiocephalic vein*, when that vein is present, just before it reaches the right auricle of the heart.

E. Lymph Nodes and Organs

In addition to the lymphatic channels and their modifications in the form of enlarged sinuses and pulsating hearts, there are present throughout the lymphatic system numerous *lymph nodes* particularly in mammals, as well as certain localized organs and tissues of a predominately lymphatic character, such as the spleen, bone marrow, the "fat bodies" of hibernating animals, the tonsils, and Peyer's patches in the small intestine.

Lymph nodes, or follicles, are structural units of lymphoid character, encapsuled in a tangle of reticular connective tissue, crowded with leucocytes, and supplied with afferent and efferent lymphatic capillaries. In these substations not only the filtering of lymph is accomplished, but also leucocytes here undergo both dissolution and renewal by mitosis.

The total aggregate of lymphoid tissue in the body is very great. It is present, for example on the floor and roof of the amphibian mouth, and in mammals becomes specialized into the tonsilar ring, made up of palatine, lingual, and pharyngeal or "adenoid" elements which guard the gateway of the alimentary and respiratory tracts against bacterial invasion. Peyer's patches in the lining of the intestine are also lymphoid areas which perform a similar protective service as "intestinal tonsils."

The thymus glands of mammals, after having sowed their possible endocrinal "wild oats" during the period of body growth, reform and join the numerous company of lymphatic organs.

The largest and most constant of the lymphatic organs is the *spleen* that lies encapsuled in the body cavity of vertebrates. This organ, which in man attains an average weight of seven ounces, is not only a center for the filterage and rejuvenescence of leucocytes, but of erythrocytes as well. Accessory spleens, or *hæmolymph nodes*, varying in size from a millet seed to a pea, are distributed in the connective tissues at various places throughout the body.

IV. THE HEART

The heart is essentially a modified blood vessel in which the tunica media, here a peculiar kind of muscle tissue different from that found anywhere else in the body, plays the principal rôle. While compressing muscular movements of the body are largely responsible for the propulsion of lymph through the lymphatic channels, the heart is the indispensable pump by means of which the circulation of the blood is accomplished.

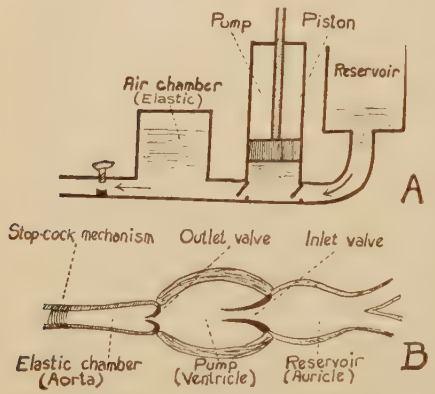


Fig. 285.—The various parts of a force pump (*A*), compared with the corresponding parts of the left ventricular pump of the heart (*B*). (After Keith.)

Amphioxus, in which the circulatory apparatus is so primitive that neither red blood corpuscles nor an accessory lymphatic system are present, has no heart at all, but the ventral blood vessel that extends between the liver and the gills, is contractile enough to propel the blood forward. It is this part of the ventral aorta which marks the location of the future vertebrate heart. From such a beginning the vertebrate heart passes through a series of modifications of increasing complexity, until eventually there is evolved the four-chambered mammalian heart.

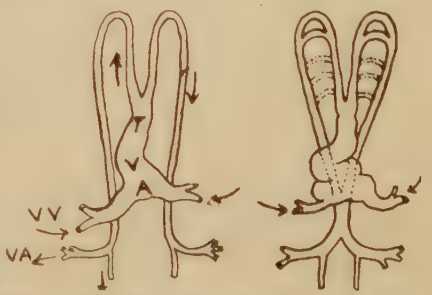


Fig. 286.—Diagrams illustrating the arrangement of the primitive heart and aortic arches. *A*, auricle; *T*, truncus; *V*, ventricle; *VA*, vitelline artery; *VV*, vitelline vein. (From Huntington, after Heisler.)

Any heart consists of two kinds of chambers, a thin-walled *receiving chamber* where the returning blood collects, and a thick-walled, muscular *forwarding chamber*, separated from the former by valves, which prevent the retreat of the blood when the muscular walls contract (Fig. 285).

The mammalian heart is double in three respects, namely: anatomically, in that it is structurally two ventricle-auricle systems together; physiologically, in that two different pumps are involved, that is, one for the distribution of the blood to the lungs for aëration, and the other, over the body for general utilization (Fig. 272); and embryologically, since the heart arises, as will be pointed out later, from the union of two vitelline veins (Fig. 286).

1. Venous Hearts

The relatively small heart of fishes, consists typically of a series of four connected chambers through which only venous, or non-aërated blood passes, since the spent blood, sent forward from the heart to the gills for aëration, must make the grand tour of the body, and become again non-aërated, before it is returned to its starting point in the heart.

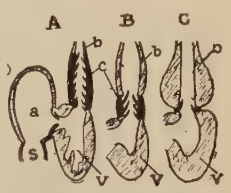


Fig. 287. — Schematic long section through the heart of fishes to show the relation of the conus and bulbus. *A*, elasmobranch; *B*, ganoid; *C*, teleost; *a*, atrium; *b*, bulbus; *c*, conus; *s*, sinus venosus; *v*, ventricle. (After Boaz.)

Beginning posteriorly, the four chambers in the heart of fishes, are the *sinus venosus*, *atrium*, *ventricle*, and *conus arteriosus* (Fig. 287). The first two belong to the receiving region of the heart and are reservoirs with elastic rather than muscular walls. The ventricle and the conus arteriosus, on the other hand, are thick-walled and muscular, and constitute the forwarding pump for the blood.

In cyclostomes the four chambers are arranged in tandem fashion, but as the heart becomes relatively larger in higher fishes it kinks up, thus losing its primitive straightness and growing more compact, with some of the chambers superimposed over others. Eventually in the vertebrate series (Fig. 288), the sinus venosus is incorporated with the atrium to form the auricle, while the conus arteriosus, is absorbed by the ventricle. The conus arteriosus, or that part of the heart beyond the ventricle but still within the pericardial chamber, undergoes various modifications among the lower vertebrates before its identity is finally swallowed up by the ventricle. In elasmobranch and ganoid fishes, as well as in Dipnoi, its proximal end is supplied with valves while its distal end becomes differentiated into the thin-walled *bulbsus arteriosus*. The conus is spirally

twisted in the Dipnoi, as if the process of incorporation with the ventricle had already begun. Among teleost fishes and the amphibians, the conus assumes a lesser rôle and a more distal enlargement termed the *bulbus arteriosus*, takes its place. The

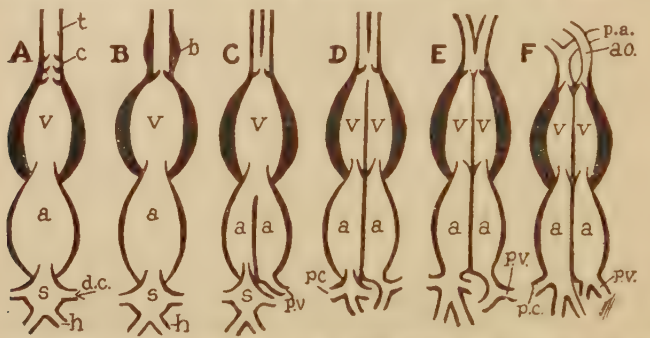


FIG. 288.—Evolution of the heart. *A*, elasmobranchs; *B*, teleosts; *C*, amphibians; *D*, lower reptiles; *E*, alligators; *F*, birds and mammals. *a*, auricle; *a.o.*, aorta; *b*, bulbus arteriosus; *c*, conus; *d.c.*, duct of Cuvier; *h*, hepatic veins; *p.a.*, pulmonary artery; *p.c.*, post-caval vein; *p.v.*, pulmonary vein; *s*, sinus venosus; *t*, truncus arteriosus. (After Kingsley.)

walls of the bulbus arteriosus are elastic and may have to do with regulating the back pressure of the blood as it is forced into the near-by capillaries of the gills.

2. Transitional Hearts

With the introduction of lungs there is initiated a new and shorter circuit, whereby aërated blood is returned directly to the heart before making the excursion of the body. The pulmonary blood is poured into the left side of the common atrium, a partition having developed which divides the original receiving chamber into two. Thus, in the Dipnoi and amphibians, which accomplish the precarious transfer from gills to lungs, there is developed what may be regarded as a heart and a half, or a heart with two atria or auricles and one ventricle. The auricular partition is incomplete in the Dipnoi, so that a mixture of aërated and non-aërated blood results within the auricles of the heart through the so-called *foramen ovale*. In amphibians, although the auricular partition is complete, the blood becomes mixed somewhat in the common cavity of the ventricle. When sent over the body without having been revivified by a trip to the source of oxygen in the lungs, there results something comparable to burning "slag" instead of coal, which is one of the reasons why these animals are "cold-blooded."

This handicap of mixed blood within the ventricle of the amphibian heart is partially avoided by the spongy reticular structure of the ventricular chamber, as well as by the rapidity of the heartbeat, which does not allow time for a thorough mixing of the two kinds of auricular blood entering at different sides of the ventricle. Therefore, every time the ventricle is filled, the mass of blood may be thought of as momentarily of three kinds, arranged in a sort of temporary stratification, with venous blood from the left auricle placed nearest the exit of the ventricle (Fig. 278), the aërated blood from the lungs farthest away from this exit, and the inevitable mixture of these two somewhere in between. As the ventricle expels the blood before these relations have either time or opportunity to change, the result is that the non-aërated blood nearest the exit fills the first possible avenues

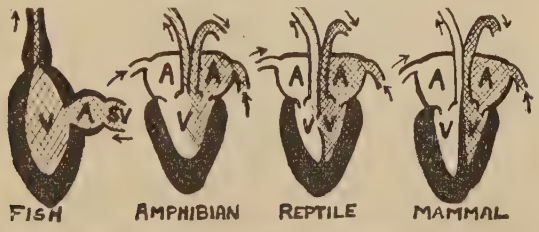


FIG. 289.—Diagrams of vertebrate hearts. *SV*, sinus venosus; *A*, auricle; *V*, ventricle. (After Hesse.)

of escape after leaving the heart, which are the pulmonary arteries leading to the lungs (the VIth embryonic arterial loop, Fig. 277, C). The intermediate mixed blood, unable to enter the already filled pulmonary arteries, is forced along into the next available blood vessels, which are the aortic loops (IVth embryonic arterial loops) distributing blood generally over the body, while the best aërated blood of all in the bottom of the ventricle, being the last to emerge and finding all other passage-ways crowded full, passes on to the carotid arteries (IIIrd embryonic arterial loops) that supply the brain. Thus the brain, that always needs the best available aërated blood, is in the way of obtaining it, even in such unintellectual ancestors as frogs and toads.

The transition from a single to a double heart is further shown by the reptiles (Fig. 289), which have come to forsake entirely the gill method of respiration, but, with the exception of the Crocodilia, have not yet arrived at the estate of a complete double

heart. Among reptiles a partition forms in the ventricle that tends to keep separate the aërated blood returning from the lungs by way of the left auricle to the left side of the ventricle, from the venous blood of the body entering the right side from the right auricle. This partition is incomplete in most reptiles, so that there still exists some degree of mixture between the right and left ventricles through the *foramen of Panizzæ* (Fig. 290). Non-aërated blood from the right ventricle goes out not only to

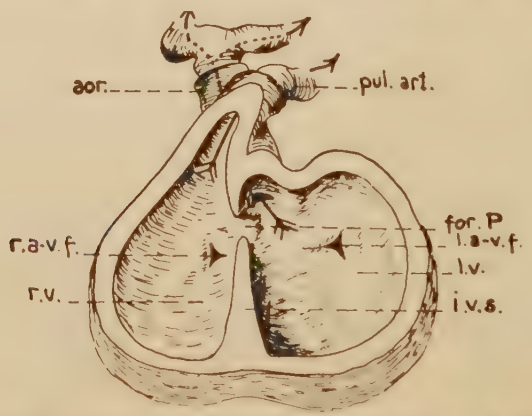


FIG. 290.—Human heart of a 7.5 mm. embryo, cut open to show relation of parts. *aor.*, aorta; *for.P*, foramen of Panizzæ; *l.v.*, left ventricle; *i.v.s.*, inter-ventricular septum; *l.a-v.f.*, left auriculo-ventricular foramen; *pul. art.*, pulmonary artery; *r.a-v.f.*, right auriculo-ventricular septum. (After Kollmann.)

the lungs but also through the right aortic loop where it joins the aërated blood from the left aortic loop that has come from the left ventricle, to form the dorsal aorta, or the main distributing trunk of the body. The result is that in reptiles, although the blood is kept unmixed as far as the dorsal aorta, there is still mixed blood being distributed over the body with a corresponding inevitable sluggishness of behavior.

3. Double Hearts

In the Crocodilia the foramen of Panizzæ becomes finally obliterated and two complete hearts, superficially incorporated into one, are established. One of these hearts is made up of the more powerful left ventricle with the right auricle, and constitutes the forwarding and receiving apparatus for the major circuit over

the body, while the other is the smaller right ventricle with the left auricle that takes care of the minor respiratory circuit of oxygen supply to and from the lungs.

Aërated and non-aërated blood, which in amphibians is mixed within the heart itself, and also in reptiles when the aortic loops join to form the dorsal aorta, is kept separate among birds and mammals as far away from the heart as possible, until the capillaries are reached.

The heart of a bird is proportionately larger than that of any other vertebrate, for an especially efficient pump is required to keep the aërial machinery of these strenuous animals going. Among mammals also small forms have relatively larger hearts than large forms. Moreover, in the same animal the proportionate size of the heart decreases with the relative decrease of heat-dispensing body surface that accompanies growth. For example, the weight of a newly-born rabbit's heart has been found to be 5.9 per cent of the total weight, while that of an adult rabbit is 2.8 per cent.

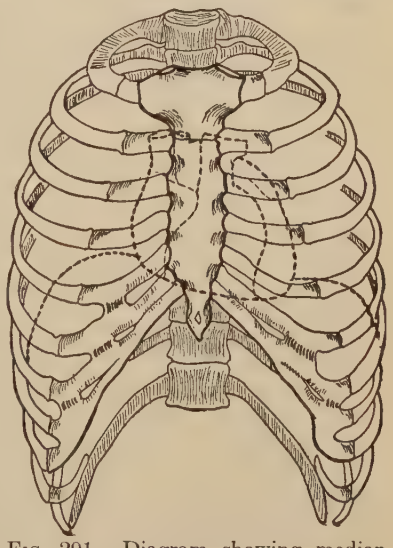


Fig. 291.—Diagram showing median position of heart in dotted outline. (After Spalteholz.)

The position of the vertebrate heart is always ventral to the digestive tube, and in gill-breathing vertebrates is far anterior. When the head of a fish or a salamander is cut off, the heart is usually included with it. In higher vertebrates as a neck evolves there is a backward migration of the heart until in such long-necked forms as swans and giraffes it comes to lie a long distance from its ancestral location and is much more centralized with reference to the body. To have "the heart in the mouth" is, therefore, a sort of ancestral sensation that should not disquiet a comparative anatomist. The human heart is popularly located by tragic actors and sentimental lovers on the left side, because the throbbing point of the cone-shaped ventricular part normally projects from behind the ster-

num toward the left side where it is most readily felt. It is in reality median in position (Fig. 291).

The adult human heart weighs not far from ten ounces, and is approximately the size of the clenched fist. In shape it is never "heart-shaped," according to the dictates of popular fancy, but a flattened cone. There have been many other popular misconceptions associated with the human heart from time immemorial, such as "a good man out of the treasure of his heart bringeth forth that which is good," and "the heart is deceitful above all things and desperately wicked." It would be just as appropriate, although less glamorous, for lovers who now pledge their hearts to each other, to pledge their livers instead, but the heart has been so long regarded as the citadel of motives and affections that the vocabulary of romance would be bereft without it.

4. The Work of the Heart

In order to accomplish its mission, blood must be kept in constant motion. That this is done is shown by the familiar fact that from any wound, however slight, which makes a break in the circulatory channels, the blood immediately flows out. In amphioxus, and in certain annelid worms, a constant flow is brought about simply by the contraction of arterial blood vessels, but in vertebrates generally, owing to the enormous expanse of capillaries developed, contraction of the arterial walls is not sufficient to keep the blood in motion, and a heart becomes necessary.

As has been indicated, the heart acts both as a force pump (Fig. 285), filling the arteries from the ventricles, and as a suction pump, drawing venous blood into the auricles.

The rate of flow is not the same in all parts of the body. It is most rapid in the aorta where the initial impulse from the heart-beat is most strongly felt, and slower in the capillary area because here, although the individual channels are much smaller, the total stream bed is much greater, so that the result is the same as when a rapidly flowing stream, confined within narrow banks, loses its momentum upon spreading out into a lake. The rate of flow is faster of course when the animal is active than when quiet. The contractions of the heart of a hibernating fish, for example, may fall from over 100 per minute, to two or three, and that of a mouse, whose normal heart beat is about 175 per minute may, when frightened, go up to 600 per minute.

From a man's heart when he is sitting quietly there is forced into the aorta about five pints of blood per minute, an amount which, upon violent exercise, may rise to an output of thirty-five pints per minute. Since the total amount of blood in a human adult is approximately only ten to fourteen pints, it is evident that, while undergoing moderate exercise, the entire blood of the body passes through the heart probably at least twice every minute. Thus, by the most liberal estimates, the strenuous red blood corpuscles, in their brief lifetime of less than two weeks, travel many miles.

The constancy of flow is aided not only by the frictional resistance of the moving blood against the inside of the blood vessels, but also by the adjustable variations in pressure upon the blood stream exerted by the contractile walls of the blood vessels under the regulatory stimulus of the involuntary nerve endings, or "stop-cocks," that supply them (Fig. 275). Although the heart beats in successive throbs, there is maintained a constant flow of blood, because the pressure is naturally higher in the arteries than in the veins. If the varying work of the heart was not regulated by some automatic device for adjusting blood pressure and controlling the flow, disaster would surely follow whenever in the countless exigencies of life, a sudden extra load is thrown upon this faithful pump. "As these terminal arteries number tens of thousands, and each of them is regulated and controlled, one can conceive how complex the stopcock system of the human machine is" (Keith).

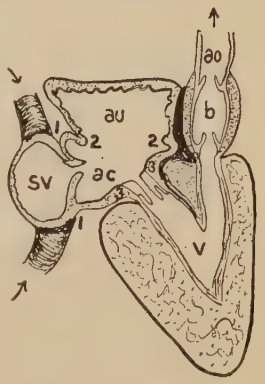


Fig. 292.—Diagrammatic section of a heart to show the location of the timing mechanism. *ac*, auricular canal; *ao*, aorta; *au*, auricle; *b*, bulbus; *sv*, sinus venosus; *v*, ventricle; *1,1*, sinu-auricular junction; *2,2*, auricular junction with canal; *3,3*, bundle of His. (After Keith.)

The tireless beat of the heart itself is probably initiated and regulated at the *sinu-auricular node* (Fig. 292). This "pace setter of the vertebrate heart" is a narrow zone of fibrous tissue that marks the transitional region between the sinus venosus and the atrium in the fish heart, and which becomes incorporated as a part of the auricle in higher vertebrates.

Another indispensable part of the mechanism of the heart is

the *auriculo-ventricular node*, a dense network of cardiac muscle fibers, connecting the auricular and ventricular walls, and acting somewhat like the "timer" in an automobile. Across this bridge the initiatory stimulus, originating in the sinu-auricular node, is transmitted to the ventricle and completes the heart beat. The

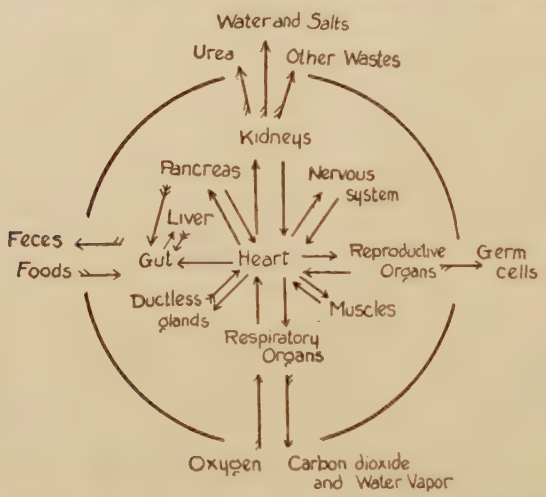


FIG. 293.—Scheme of circulation of materials in the animal body. Tail-less arrows represent blood vessels. Tailed arrows represent ducts of glands, or blood vessels leaving ductless glands. Arrows representing materials entering or leaving the body are tailed on one side only. (From Woodger's *Elementary Morphology and Physiology*. Oxford University Press.)

auriculo-ventricular node was discovered in the human heart by His in 1893, and is consequently known as the *Bundle of His*.

The central relation of the heart to other parts of the body is indicated in Fig. 293.

5. The Valves of the Heart

The most constant valves of the heart in the vertebrate series are the *auriculo-ventricular valves*, which separate the receiving auricle from the forwarding ventricle. They are present in all vertebrates and are kept from reversing under the pressure of the contracting ventricle by tendinous guys called *chordæ tendineæ*, that are anchored in the muscular walls of the ventricle (Fig. 294).

There are two auriculo-ventricular valves in the heart of fishes, but in the double hearts of mammals there are five present, two

between the auricle and ventricle on the left side (*bicuspid*) and three (*tricuspid*) on the right side.

The bicuspid valves are commonly known as *mitral valves* from a fancied resemblance to a bishop's mitre. It was Huxley who once humorously said that he could always remember the location of the mitral valves on the *left side* of the heart, because he "never knew a bishop to be on the right side."

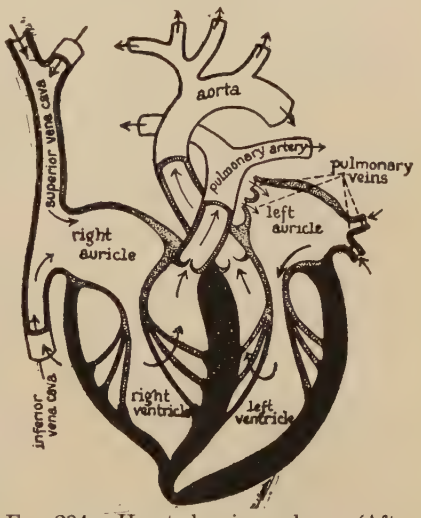


Fig. 294.—Heart showing valves. (After Jammes.)

The semi-lunar valves of the conus region are best seen in elasmobranchs and ganoids, where as many as eight rows may appear in some species. They are cup-like pockets, lying flat against the inner wall as the blood passes out over them, but which fill immediately and block the passage-way when the blood attempts to retreat. Similar valves guard the exit from the heart to the pulmonary arteries and to the aorta in the higher forms.

In the primitive heart of fishes, where the sinus venosus still persists as a distinct chamber, there is present between the sinus venosus and the atrium, a pair of *sinu-atrial valves*, that, like swinging doors, allow the blood to pass either way. This does no harm since both sinus and atrium have the common function of acting as reservoirs for returning blood. Between atrium or auricle and ventricle, on the other hand, one-way traffic must be maintained when the muscular ventricle forces out the blood, consequently the mitral and tricuspid valves with their chordæ tendineæ, swing only so far and no farther.

6. Evolution of the Heart

The first step in the differentiation of the vertebrate heart, is encountered in the larval stage of the lamprey eel, *Ammocœtes*. The arterial blood vessel lying between the liver and the gills,

which represents the prophetic "heart" of amphioxus, becomes somewhat enlarged and modified. These changes involve first a *constriction* into the four chambers that characterize the typical heart of fishes, and second, a kinking of these chambers, necessitated by rapid growth within crowded quarters, so that they no longer lie in a straight line. In the ammocoetes stage the heart is still in the common body cavity with the liver, intestine, and other organs, but among fishes generally a *transverse septum* forms and ever after the heart is housed within the privacy of an enveloping space of its own, the *pericardial cavity*. In elasmobranch fishes the *pericardio-peritoneal canal*, a slitlike opening between the pericardium and the body cavity, is the last phase in the establishment of pericardial independence.

The next evolutionary step along with constriction and kinking is the *differential thickening of the tunica media*, by which means the thick-walled ventricle becomes established as an effective pump. The chambers of the elongated heart next *telescope together*, so that the sinus venosus, which is really an antechamber of the atrium, becomes incorporated in the atrium to form the auricle, and the various modifications of the conus arteriosus, become combined as a part of the ventricle itself. These changes are accompanied and followed by a gradual *doubling of the heart*, initiated in the Dipnoi and Amphibia by a partition which divides the atrium into two auricles, and is continued in the reptiles by partitions that bring about in similar fashion the formation of two ventricles, an end first completely attained in the Crocodilia, which is also characteristic of all birds and mammals (Fig. 288).

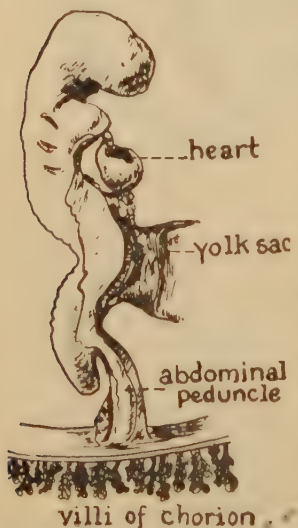


Fig. 295.—Human embryo of the third week showing gill clefts and external heart. (After His.)

7. Embryology of the Heart

The human heart in its development is reminiscent of thee volutionary differences that are seen in the vertebrate series. Toward

the end of the second fetal week it appears as right and left cardiac tubes which become fused into a median blood vessel, like that of amphioxus, soon kinking and going through the historical paces set by vertebrate forebears until, sometime before birth, with the obliteration of the foramen of Panizzæ in the septal wall separating the ventricles, it becomes a complete, double, four-chambered, mammalian heart.

At first the heart is outside the body walls (Fig. 295), but eventually moves in, through adjustments in relative growth relations,

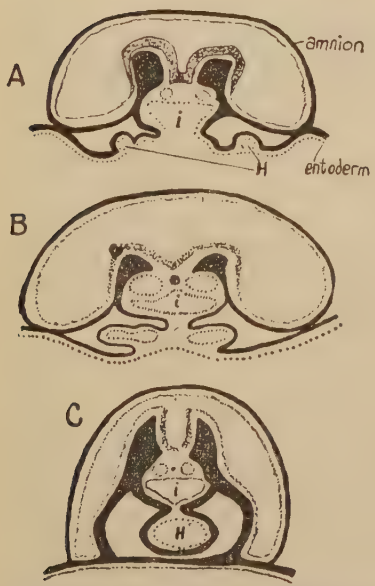


Fig. 296.—Diagrams illustrating the formation of the heart in the guinea pig. The mesoderm is represented in black, *i*, intestine, *H*, heart. (From McMurrich, after Strahl and Carius.)

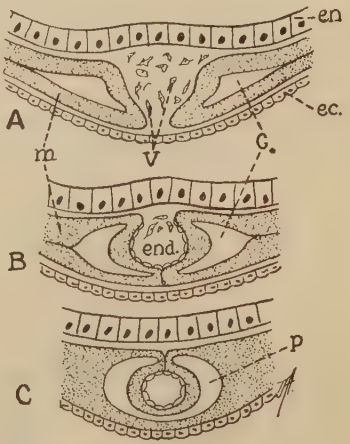


Fig. 297.—Diagrammatic cross sections of developing heart. In *A* the descending mesothelial plates have nearly met, with a number of vascular cells between them. In *B* the plates have met ventrally, forming the ventral mesocardium; most of the vascular cells have been utilized in forming endocardium, *end.* In *C*, the plates have met dorsally, the ventral plate has disappeared, and the pericardium, *p*, has been established. *C*, cœlome; *ec.*, ectoderm; *en.*, entoderm; *end.*, endocardium; *m*, mesoderm; *p*, pericardium; *V*, vascular cells. (After Kingsley.)

and takes up a permanent centralized position inside the protecting body walls.

The formation of the heart from its double components, and its enclosure within the pericardium, are shown in Figs. 296 and 297.

V. THE ORIGIN OF THE CIRCULATORY SYSTEM

The beginnings of the circulatory apparatus appear very early in development since the transport of foodstuff to the focal point

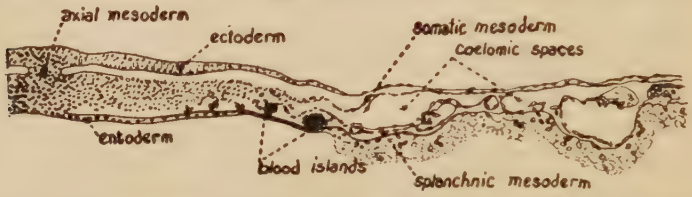


FIG. 298.—Transverse section through the primitive streak of a chick of about twenty-four hours, showing the formation of blood vessels and blood. The section extends from the mid-line nearly half across the area vasculosa. (After Kellicott.)

where the new animal is to materialize, is a primary necessity. In the chick (Fig. 298) as soon as the fertilized egg has undergone preliminary cleavage, and the potential pioneer cells thus formed have arranged themselves into the primary germ layers, certain peripheral cells of the splanchnic mesoderm become differentiated as *blood islands*. These consist of blood-forming, or hæmopoietic cells, and of flat endothelial cells which surround them to make the lining of the future blood channels.

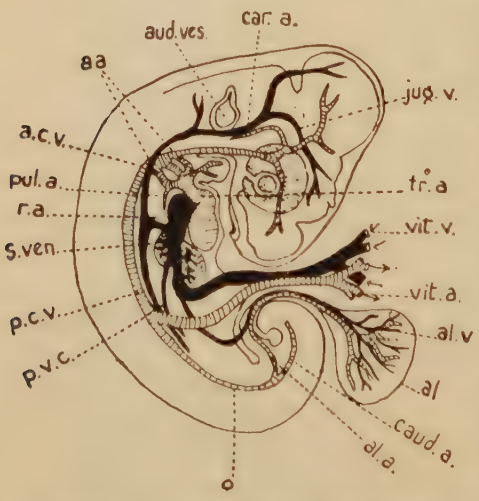


FIG. 299.—A diagram showing arrangement of blood vessels in a chick embryo at the end of the fifth day of incubation. *aa*, aortic arches; *al.a.*, allantoic artery; *car.a.*, carotid artery; *caud. a.*, caudal artery; *pul.a.*, pulmonary artery; *vit.a.*, vitelline artery; *r.a.*, right auricle; *aud. ves.*, auditory vesicle; *s.ven.*, sinus venosus; *tr.a.*, truncus arteriosus *al.*, allantois; *al.v.*, allantoic vein; *a.c.v.*, anterior cardinal vein; *p.c.v.*, posterior cardinal vein; *p.v.c.*, posterior vena cava; *jug.v.*, jugular vein; *vit. v.*, vitelline vein. (Modified from Marshall.)

The blood islands, which form a halo around the embryo on the surface of the yolk between the entoderm and the splanchnic mesoderm, are soon organized into a network of

capillaries, that coalesce into a pair of definite blood vessels, the *vitelline veins*, one on either side. These lead directly into the growing body of the embryo where they unite in a common trunk, which is the beginning of the future heart (Fig. 286). From this, two primary aortic loops emerge and, after running back parallel within the body, continue outward to the capillary field as the *vitelline arteries*. This primary circuit, the first to be established in vertebrates with well-developed yolk, is called the *vitelline circulation* (Fig. 299).

Budding off from the vitelline circuit within the enlarging body are secondary trunk lines which extend to and from both

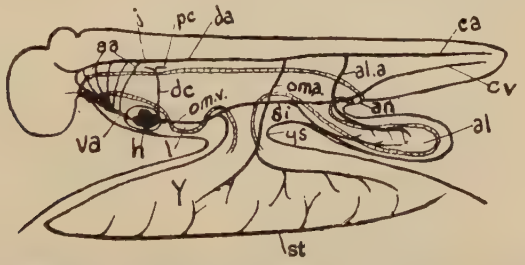


Fig. 300.—Diagram of embryonic circulation in a large yolked vertebrate. *aa*, aortic arches; *al*, allantois; *al.a*, allantoic artery; *an*, anus; *ca*, caudal artery; *cv*, caudal vein; *da*, dorsal aorta; *dc*, duct of Cuvier; *h*, heart; *j*, jugular vein; *l*, liver; *om.a*, omphalomesenteric vein; *pc*, postcardinal vein; *si*, subintestinal vein; *st*, sinus terminalis; *va*, ventral aorta; *y*, yolk; *ys*, yolk stalk. (After Kingsley.)

the head and tail regions. These, together with components salvaged from the temporary vitelline circuit, are destined to make up the permanent *systemic circulation* (Fig. 300).

Still a third circulation, the *allantoic*, is necessary during the development of the higher vertebrates to meet the conditions imposed by embryonic life within an amnion. It consists of a pair of *allantoic arteries*, arising from the posterior region of the aortic loops, which pass out to supply the temporary sac-like allantois. The returning *allantoic veins* enter the heart close to the vitelline veins. In mammals the allantoic arteries and veins become the *umbilical arteries* and *veins*, and form the nutritive and respiratory bridge through the placenta between the fetus and mother. The *placenta* itself is a compound capillary organ of double derivation (Fig. 301), the part from the allantois of the embryo interdigitating into the uterine wall of the

mother so that by osmosis there can occur a transfer of materials between the blood of the two. In the earliest known embryo in which the circulation is described (Fig. 117), the allantoic circulation appears to take precedence over the vitelline circulation, a state of affairs not unexpected, since in mammals the yolk sac and accompanying vitelline blood vessels play a rôle of decreasing importance.

The need of the vitelline circuit wanes with the vanishing yolk, while the allantoic circuit becomes useless upon hatching or at birth. Thereafter the systemic circuit takes up its functions and maintains them throughout life. The precarious

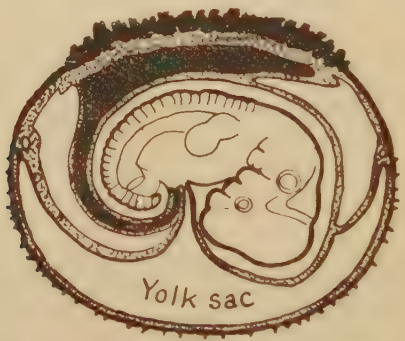


Fig. 301.—A rabbit embryo twelve days old. The allantois and placenta are in black. (After Marshall.)

transition from embryonic to permanent circulatory devices, involves profound modifications, and in mammals, where the umbilical cord is severed at birth, it is very abrupt.

Three pairs of venous trunks, which undergo various fates, open into the embryonic heart. The first are the *ducts of Cuvier*, bringing in systemic blood from the head, body, and limbs; the second, the *allantoic*, or *umbilical veins* from the allantois or placenta; and the third, the *omphalomesenteric veins*, formed by the union of the vitelline veins from the yolk and the mesenteric veins from the digestive tube, which at first is continuous with the yolk sac. The allantoic veins cease to function with the transfer of respiration from the extra-embryonic allantois to the lungs within the body. The omphalomesenteric veins, just before they enter the heart, become surrounded by the growing tissue of the liver in which they break up into a capil-

lary network (Fig. 302). The right vein degenerates, but the left persists as the *hepatic portal vein* between the intestine and

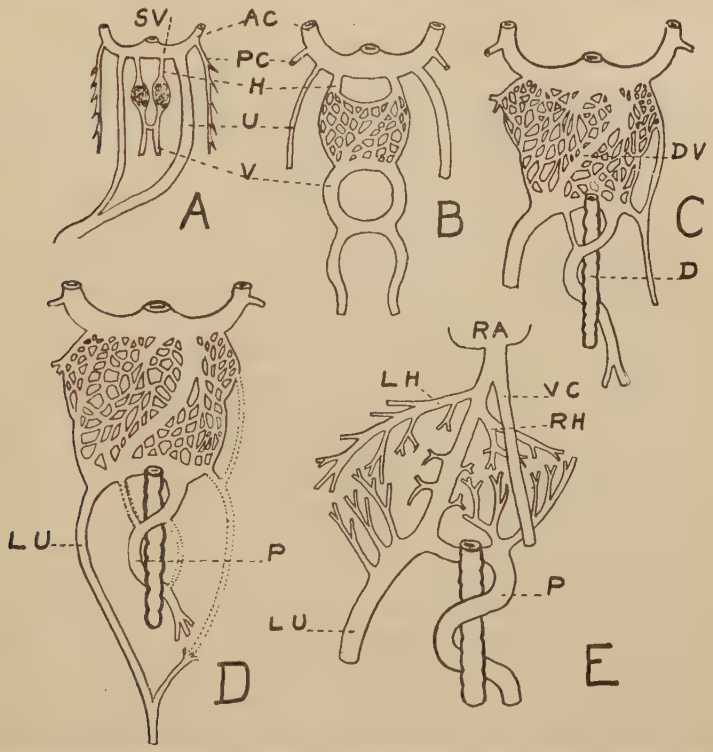


FIG. 302.—*A-E*, diagrams of the development of the hepatic portal system from dorsal view. *AC*, anterior cardinal vein; *D*, duodenum; *DV*, ductus venosus; *H*, hepatic vein; *LH*, left hepatic vein; *LU*, left umbilical vein; *P*, portal vein; *PC*, postcardinal vein; *SV*, sinus venosus; *U*, umbilical vein *V*, vitelline vein; *VC*, vena cava; *RA*, right auricle; *RH*, right hepatic vein. (After Huntington.)

liver. The proximal ends of both the right and left omphalomesenteric veins remain between the liver and the heart, where they are known as *hepatic veins*.

CHAPTER XIII

THE RELEASE OF ENERGY (RESPIRATORY SYSTEM)

I. IN GENERAL

1. The Respiratory Environment

Every living thing of which we have any knowledge exists on the planet Earth, at the bottom of a vast atmospheric ocean. Air envelops not only all land surfaces but also extends to the uttermost depths of every body of water, large or small, so that aquatic as well as terrestrial animals and plants find themselves bottom-dwellers with respect to the all inclusive atmosphere. Oxygen of the air forms the indispensable setting for the drama of life. Of all organisms, only the extremely specialized group of anærobic bacteria seem to be able to live without it.

Although the atmospheric envelope is enormously extensive in every outward direction, the only part of it occupied by living things is comparatively the merest film in thickness, where the atmosphere comes in contact with the solid earth. The greatest vertical distance from the atmospheric floor reached by any organism, has been attained by modern aviators, who have outstripped even soaring birds. However, the exceptional altitudes gained by these human pioneers of the air must be regarded as insignificant in extent when compared with the distances involved in the horizontal exploration of the earth's surface.

Probably eighty per cent of all animals breathe *free air*. This category includes mammals, birds, reptiles, most amphibians, the great fraternity of tracheate arthropods, besides certain gasteropods among the molluscs. In the minority, innumerable aquatic invertebrates, fishes, and perennibranchiate amphibians, habitually breathe air that has been *dissolved in water*, that is, air which occupies the invisible interstices between molecules of water.

Some animals, for example, whales and pulmonate snails, live habitually in water but come to the surface for free air,

while a few exceptional land animals, such as the terrestrial isopod *Porcellio*, and the land crab *Birgus*, still retain, at obvious disadvantage, the primitive aquatic method of taking air in water by keeping their gills moist, although they have deserted the water as a medium in which to live.

Since there is more available oxygen in free air than in air dissolved in water, free-air breathers in general exhibit more energy than aquatic forms, living as they do in a more favorable respiratory environment. Sea water, for example, has been found to contain from five to seven cubic centimeters of oxygen per litre, flowing fresh water, six to eight cubic centimeters, and free air over 200 cubic centimeters per litre.

2. The Exchange of Gases

When the Declaration of Independence was signed no one knew that respiration is a form of slow combustion, dependent upon a component in the air called *oxygen*. Lavoisier made this clear for the first time in 1777.

The exchange of gases which we term *breathing* is primarily a physical rather than a biological phenomenon. The taking in of oxygen is a process of passive diffusion that ceases as soon as the oxygen within the cells concerned balances with that outside. As a result of taking in oxygen, tissues are slowly broken down, while the energy used to build them up is released, much as "stored sunshine" from carboniferous plants is recovered in the form of heat-energy, whenever these fossils which we call "coal," are burned under a draft of air. In both burning coal and the living body, the most conspicuous product of combustion is *carbon dioxide*. This is given off directly, since it acts as a poison when retained. In fact the removal of carbon dioxide is so urgent a matter that no animal can "hold its breath" very long without being compelled by an imperative stimulus quite beyond its control, to resume breathing movements. This powerful stimulus that insures the continuous working of the mechanism of respiration is an excess of carbon dioxide in the blood.

Neither the carbon dioxide of metabolism nor the oxygen of the air can be stored within the body, as food can. Consequently, although respiration may be reduced to a minimum at times of exceptional inactivity, it cannot cease during life, a fact which

sharply distinguishes a living, energy-producing organism from a dead organism.

Respiration is an excretory function, with reference to carbon dioxide, for, in the maintenance of life, it seems to be of more importance to get rid of the deadening carbon dioxide than to acquire more oxygen, although the two processes go hand in hand and are both indispensable. Aquatic animals are easily killed in carbonized water, even if oxygen is present in sufficient amount for breathing. The excretory phase of respiration may be further demonstrated by the fact that when hydrogen sulphide is injected into the blood it is eliminated through the lungs.

Physiologists distinguish between *external* and *internal* respiration. The former is concerned with the gaseous exchange of oxygen and carbon dioxide between blood and air. The latter has to do with the essential transfer between blood and the tissues, or ultimate cells of the body which constitutes the effective part of respiration, and brings about the release of energy characteristic of life. The distinction between external and internal respiration disappears in small animals which have not elaborated a circulatory system, and the transfer of gases takes place directly through the undifferentiated surface of the organism in contact with its atmospheric environment.

3. The Essentials for any Respiratory Device

In order to utilize the oxygen of the air any living mechanism that has evolved far enough to have a true circulatory system, must meet the following conditions: (1) the blood that is to receive oxygen must be separated from the air by a retaining cellular wall; (2) the wall must be sufficiently permeable to permit easy osmosis of gases; (3) the wall must be kept moist in order to allow for thinness and permeability without drying up upon exposure to air; (4) the total walls, or respiratory surfaces, must be extensive enough in area to insure an adequate osmosis of oxygen for the organism concerned; (5) a current of fresh air must be made to pass repeatedly across the respiratory surface. These conditions are met in a variety of ways by different animals.

4. Different Kinds of Respiratory Mechanisms

In the more primitive aquatic forms, diffuse breathing through the *skin* precedes localized breathing through specific respiratory

organs, such as the gills or lungs, although both methods may be employed simultaneously, as in the Amphibia. Diffuse breathing is a decided handicap, since the necessarily delicate integument in animals that employ this method, is not only subject to mechanical injuries, but its possessor must remain under water in order to escape the disastrous effects of drying air.

The two most successful breathing mechanisms among terrestrial animals are tracheal tubes and lungs. *Tracheal tubes*, which have been elaborated by the great specialized host of insects, consist essentially of ramifying tubes of inturned integument that admit air to the immediate neighborhood of the blood within the body (Fig. 303). *Lungs* are air sacs in intimate proximity to vascular networks, with elaborate modifications for increasing the respiratory surface without harmful exposure to the dessicating effects of outside air.

FIG. 303. — Respiratory tracheal tubes of a honey bee. (After Hertwig.)

Sometimes the intake of oxygen and the outgo of carbon dioxide are effected by different parts or organs of the body. In many Protozoa, for example, oxygen is admitted through the *surface ectoplasm*, while the *contractile vacuoles* are concerned directly with the disposal of accumulating carbon dioxide. Aquatic amphibians, although acquiring oxygen principally by means of lungs, give off carbon dioxide, which has great solubility in water, largely through the skin.

In addition to the gills, skin, and lungs of vertebrates, the tracheal tubes of insects, and the more primitive ectoplasmic devices of the Protozoa, any representative museum of respiratory inventions would be bound to contain a long array of devices that different members of the animal kingdom have to present, solving the universal biological problem of gas exchange. To cite only a few and the more familiar of these devices among invertebrates, there may be mentioned the *ciliary system* of sponges; the *aboral tentacles* of starfishes; the *respiratory tree*, safe within the body cavity of the mud-inhabitating sea cucumbers; the curious *respira-*

FIG. 304.—Goggle-eyed *Periophthalmus*, a fish which climbs out of water on the aërial roots of mangrove trees to catch insects. (After Kraepelin.)

tory bladder of the rotifers; the *integument* of the sinuous waving annelids; the expansive *mantle* of molluscs; and the compact *lung books* of spiders; and among vertebrates, the curious *respiratory tail* of the goggle-eyed *Periophthalmus* of Indo-Pacific mangrove swamps (Fig. 304), a fish that remains for hours out on land with only its highly vascular tail submerged in water. *Hylodes martenicensis*, an Antillean frog which undergoes its entire metamorphosis within the egg, also accomplishes breathing during this critical period by means of a broad respiratory tail.

Fig. 305. — Branching respiratory barbules of the larva of a South American toad, *Xenopus*. (From Wiedersheim, after Bles.)

It must not be forgotten, moreover, that in all reptiles, birds, and mammals, the *allantois* is provided as a temporary breathing organ during embryonic life. This highly vascular device for gas exchange is absorbed before hatching in the case of reptiles and birds, and in mammals is lost with the placenta at birth.

Fig. 306.—Hairy frog, *Trichobatrachus*, whose "hairs" are probably integumentary respiratory devices. (After Boulenger.)

The lungless salamanders which swallow air have a *pharyngo-esophageal capillary network* that acts as an accessory respiratory contrivance to supplement the integument and gills, while the larva of the South American toad, *Xenopus* (Fig. 305), possesses a kind of *integumentary chin whiskers* which, according to Bles, are respiratory in function. Also in the case of the hairy frog, *Trichobatrachus* (Fig. 306), the "hairs" probably serve the same purpose.

Fig. 307.—The gills of the climbing perch, *Anabas*, exposed to show how they are protected beneath the operculum so as to be kept from drying up during the excursions out of water which this curious fish makes. (After Hilzheimer).

Certain fishes, such as *Callichthys*, *Hypostomus*, *Doras*, and *Cobitis*, breathe by means of a *vascular rectum*, alternately sucking in and squirting out water, and turtles in a similar fashion utilize a pair of lateral *cloacal sacs* with capillary walls.

The air-breathing labyrinthine fishes, for example, *Polycanthus*,

Osphromenus, Trichogaster, Macropodus, Ophiocephalus, Clarias and the East Indian climbing perch, *Anabas* (Fig. 307), have a peculiar enlargement of the gill cavity, behind the eyes and dorsal to the first and second gill arches, in which pocket-like space there is crumpled a much-folded vascular structure, the *labyrinth,* that meets all the requirements of a respiratory organ, under the difficult conditions of enveloping mud.

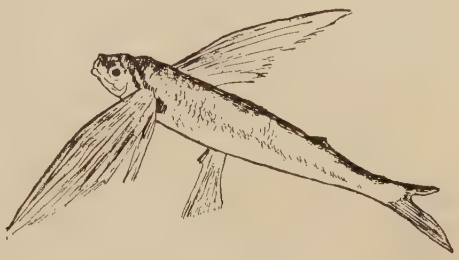


Fig. 308.—A flying fish, *Exocœtes.* (After Hesse.)

The glimmering flying fishes, *Exocœtes* (Fig. 308), that enliven the surface of tropical waters, no doubt "hold their breath" for the brief intervals during which they forsake the water, since their gills do not seem to be supplemented by any peculiar additional breathing organs.

The *swim bladder* of fishes, as well as the accessory *air sacs* of birds, and of some fishes and reptiles, which will be more fully described later, are both connected with the function of respiration.

Finally, the *gills* and *lungs* remain to be considered.

II. GILLS

The problematical ancestral vertebrates, amphioxus and the tunicates, which are largely sedentary in habit, obtain their microscopic food through ciliary action by creating a current of water that flows into the mouth. Since the water also contains the oxygen essential to respiration, it is obvious that respiratory organs placed in the pathway of this current of water, will be most favorably located for obtaining oxygen. Thus, we find gills, lungs, and even more uncommon respiratory devices, such as swim bladders in fishes, and pharyngo-esophageal capillaries in lungless salamanders, colonizing at the anterior end of the alimentary canal. There is, in fact, an intimate relationship between the respiratory organs of vertebrates and the anterior end of the digestive tube. Originally, perhaps, the entire digestive tube shared in the respiratory function, as suggested by the rectal breathing of certain modern fishes. Surely in amphioxus, as much as the anterior

half of the tube is concerned with respiration. In most vertebrates, however, the apparatus for breathing is more restricted, although still closely connected with the pharyngeal region.

In aquatic vertebrates, for example fishes, a series of paired lateral openings, or *gill slits*, in the sides of the pharynx, make possible a dual disposal of the water that is taken into the mouth. It can either pass straight on through the esophagus to the stomach and intestine, in which case its food content is utilized, or it can stream out through the porthole-like gill slits, when the oxygen it contains may be transferred to the delicate respiratory *gills*, or branchiæ, hanging suspended within the space of these gill slits. In this way both respiration and alimentation are effected.

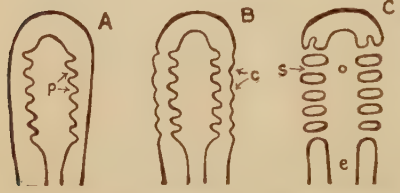


Fig. 309.—Diagrams to illustrate the formation of gill pouches, clefts, and slits. *A*, early stage, showing the outpushings of the pharynx that form the gill pouches, *p*; *B*, intermediate stage with gill pouches and in-pushings from the outside, or gill clefts, *c*; *C*, later stage, in which pouches and clefts have met and formed passage-ways, or gill slits, *s*, from the pharynx to the outside, in which the gill filaments hang suspended. (After Hyman.)

Between the gill slits in the walls of the pharynx, helping to hold them open, are skeletal parts, the so-called *gill arches*, that furnish support for the vascular gills.

During the early development of all vertebrates, a series of internal pockets, the *gill* or *pharyngeal pouches* (Fig. 309, A), push outward from the sides of the pharynx. These are lined with the same sort of endothelial tissue found throughout the alimentary canal. Meanwhile on the outside corresponding indentations or depressions in the ectoderm, the *gill clefts*, or branchial grooves (Fig. 309, B), make their appearance. Later the pharyngeal pouches and branchial grooves meet to form the closing plate which eventually breaks through in lower vertebrates to form the gill clefts, and the tissue separating them is absorbed, thus forming the *gill slits*, or pharyngeal clefts (Fig. 309, C), which complete the passage-way from the pharyngeal cavity to the outside. Finally, along the margins of the gill slits, delicate, feathery, thin-walled evaginations containing capillaries develop as *gill filaments*, or "gills," and these are the essential organs of respiration.

In general the number of pairs of gill slits varies from fourteen

in the cyclostome, *Bdellostoma polytrema* of the Pacific Coast, to only one pair, between the third and fourth gill arches, in the derotreme salamanders. The complicated branchial basketwork of tunicates forms a remarkable exception, as well as the sixty or more pairs of gill slits in the elongated pharynx of amphioxus. In reptiles, birds, and mammals, gill slits do not normally break through, although both gill pouches and gill clefts occur in the embryo.

1. Invertebrate Gills

The gills of invertebrates are not associated with pharyngeal gill slits as is the case in vertebrates, neither are they located in a special region of the body, but are found anywhere within easy access to the water. For example, certain annelid worms have gills with the *parapodia* or lateral appendages down the sides of the body (Fig. 310).

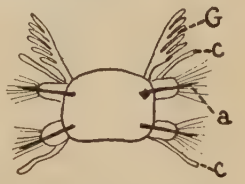


Fig. 310.—Schematic cross section of an annelid to show invertebrate gills. *a*, aciculum; *c*, cirrus; *G*, gill. (After Boaz.)

The ciliary "gills" of lamellibranch molluscs are concerned primarily with directing a stream of microscopic food toward the mouth, and are of doubtful respiratory service; while the thoracic gills of crustaceans, and the abdominal gills of larval aquatic insects are simply thin feathery expansions of the chitinous skin, enclosing tracheal tubes which in this way extend outside the body instead of being turned inside, as in land tracheates.

2. Primitive Gills of Amphioxus and Tunicates

The fact that tunicates are enveloped in a thick, non-respiratory, cellulose tunic, or mantle, makes necessary an enlarged pharyngeal basket, that forms a respiratory structure often exceeding in size all the other organs of the body. The tunicate *Phallusia* (Fig. 10), for instance, has a branchial basket perforated with several thousand gill slits, while the ghostly transparent Appendicularia, which are tunicates without a cellulose mantle and consequently with greater capacity for diffuse integumental breathing, possess only a single pair of gill slits.

Amphioxus is characterized by an exceptionally generous number of gill slits (Fig. 13), and these are bordered by primitive vascular tissue that presents much less respiratory surface than is common to the more elaborate gills of fishes and amphibians. No expansive

gill filaments are found in the "gills" of amphioxus, such as appear in higher aquatic vertebrates, so these ancestral animals are obliged to make up in number what they lack in individual area. The entire gill system of amphioxus is enclosed in a *peribranchial chamber* opening indirectly to the outside through a single ventral *atrial pore*, instead of directly through the gill slits. The walls of this chamber protect the delicate gill surfaces from the sand in which these animals burrow, while allowing the unobstructed passage of water through the gill slits.

FIG. 311.—Diagrammatic cross section through the endostyle of *Clavellina lepidiformis*, showing glandular walls, and projecting cilia standing up in the bottom of the groove. (After Seeliger.)

Since the numerous gill slits of amphioxus and the tunicates increase the hazard of the escape of food through them, the development of a device for directing bits of food past these lateral openings to the esophagus, is necessary. The modification accomplishing this end is the *endostyle* (Fig. 311), a ciliated, glandular groove in which food particles become collected together into a mucous rope, that passes along continuously into the gullet. Later in vertebrate evolution, when the endostyle is no longer needed for the purpose of steering food, this pharyngeal groove becomes transformed into the thyreoid gland with an entirely different function. The student of comparative anatomy often finds things in the morphological junk pile that have thus become utilized for purposes entirely different from those to which they were originally put.

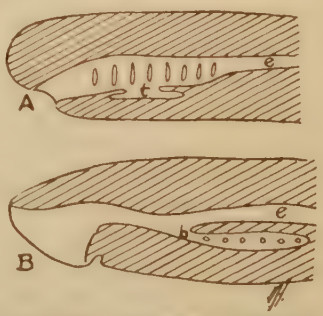


FIG. 312.—Diagram of the relation of the esophagus and respiratory tract in (*A*) *Myxine*, and (*B*) *Petromyzon*. *b*, branchial duct; *e*, esophagus; *t*, thyreoid gland. (After Kingsley.)

3. Cyclostome Gills

The arrangement of gills in cyclostomes is somewhat different from that in other fishes. A partition between the alimentary and respiratory parts of the pharynx is formed by a forward extension of the esophagus, leaving the branchial apparatus in blind lateral

pouches on the two sides (Fig. 312). Water in its passage over the gills may *enter* through the anterior gill slits instead of the mouth, which is frequently otherwise occupied on account of the suctorial habits of these animals. The gill slits are modified also by widening out into separate pockets, each of which connects with a narrowed passage-way to the pharynx as well as with one to the outside. Since gills are located in these pockets, cyclostomes are frequently referred to as *Marsipobranchs*, meaning "pouched gills."

Different species of *Bdellostoma* have from ten to fourteen pairs of gill slits. *Petromyzon* has eight embryonic pairs but only six in the adult. *Myxine* has six pairs with all the external passage-ways uniting into a common canal opening by a single pore to the outside.

4. Elasmobranch and Holocephalan Gills

The gill slits of elasmobranch fishes are lateral in position in sharks and dogfishes, but ventral in skates and rays. They open independently to the outside and are separated from each other

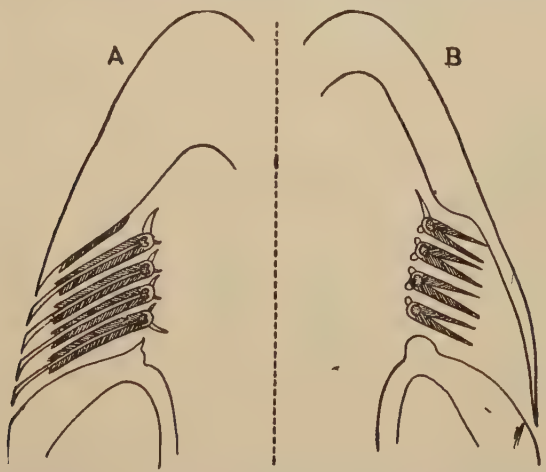


FIG. 313.—Relation of gills to branchial chamber. *A*, elasmobranch, with gill septa; *B*, teleost, without gill septa. (Modified from Schimkewitsch.)

not only by skeletal gill arches of cartilage, but also by primitive partitions attached to these arches, *interbranchial septa*, on either side of which are located the gill filaments, or gills proper. Thus, two half sets of gill filaments, *hemibranchs*, one on one septum and the other facing it on the opposite septal wall, hang within the space of each gill slit (Fig. 313, A).

The most anterior pair of pharyngeal portholes in elasmobranchs, between the mandibular and hyoid arches, develops into the *spiracles*, not far posterior to the eyes in position. The walls of the spiracles are not provided with true gills, but in some cases may support on one side at least a "false" gill, or *pseudobranch*, so-called because its blood supply is not derived, like that of true gills, direct from a branchial artery bearing "impure" blood, but from the branchial vein of the following gill arch which, having already given up its load of carbon dioxide and taken in oxygen, carries "pure" blood.

In the bottom-feeding skates and rays the spiracles open dorsally, instead of ventrally as the other pharyngeal gill slits do. They are useful, therefore, in taking the water of respiration into the branchial cavity when the mouth is otherwise occupied grubbing for food in the mud. No doubt sharks and dogfishes, which swim about freely and gracefully in the water, likewise use the spiracles upon occasion instead of the mouth as an accessory port of entry for the water of respiration.

In the primitive shark, *Heptanchus*, there are seven pairs of gill slits, with one pair of spiracles. In the cow shark, *Hexanchus*, and the frilled shark, *Chlamydoselachus*, there is one less pair of gill slits, while in most elasmobranchs the typical number, aside from the spiracles, is five pairs. The cub shark, *Carcharias*, and the mackerel shark, *Lamna*, are without spiracles.

FIG. 314.—Embryonic external gills of dogfish. (After Schimkewitsch.)

Certain larval elasmobranchs, which undergo considerable development within the eggshell before hatching, have gill filaments so long that they hang out of the gill slits as temporary *external gills*. These unusual structures may serve as absorbing organs in connection with the enormous yolks present in these eggs (Fig. 314).

The holocephalans, or strange elephant fishes, have much in common with elasmobranchs, but are characterized by having four pairs of gill slits and an *operculum*, or flap of integument, on either side extending backward from the margin of the hyoid

arch, and covering the external openings of the three anterior pairs of gill slits, leaving only the last pair open directly to the outside after the fashion of the elasmobranchs. Possibly the forerunner of this opercular flap is seen in the elasmobranch, *Chlamydoselachus*, where the skin on the anterior margin of each gill slit extends backward as a small independent protective fold, covering the opening of each gill slit (Fig. 315). This feature gives *Chlamydoselachus* the common name of "frilled shark."

FIG. 315.—A primitive shark, *Chlamydoselachus*, with external flaps for each separate gill slit. (After Schimkewitsch.)

5. Ganoid and Teleost Gills

The gill system of ganoids in some ways represents a connecting link between that of elasmobranchs and teleost fishes. There are four pairs of gill slits present, covered by an operculum which is stiffened by flat skeletal plates between two surfaces of folded integument. Outside and anterior to the operculum on either side, there is a degenerate spiracle in some of the ganoids, while on the inner surface of the operculum there is attached a small *opercular gill*, homologous neither with true gills nor with the pseudobranchs of the hyoid arch.

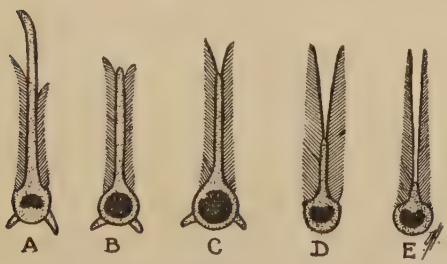


FIG. 316.—The progressive reduction of gill septa in different fishes. *A*, elasmobranch; *B*, holocephalan; *C*, ganoid; *D* and E, teleosts. (After Boaz.)

The interbranchial septa in ganoids are reduced so that the hemibranchs, placed upon them back to back on either side of a septum, are no longer in separate chambers, but occupy together a common branchial cavity (Fig. 316). The reduction of the interbranchial septa becomes complete in teleost fishes, so that the gills all lie compacted closely together in a common chamber covered by the operculum (Fig. 313, B).

The number of gill arches in both ganoids and teleosts is usually four or five pairs, although they may be reduced to three, or

even two pairs, in some of the bony fishes. Spiracles are not characteristic of teleosts.

The opercular opening becomes much diminished in such fishes as eels, thus enabling them to retain water in the branchial chamber under unfavorable conditions.

Probably the immediate reason why fishes suffocate when removed from a water environment, is not because the gills dry up at once with a collapse of the capillaries in the gill filaments, but because when out of water the gills adhere to each other, thus leaving the exposable respiratory surface reduced beyond the danger point.

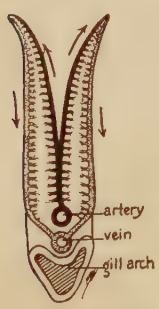


FIG. 317.—Structure of a typical gill. (After Cuvier.)

The structure of a typical teleost gill, with its relatively great expanse of respiratory surface within a small compass, and the arrangement of its capillaries are indicated in Fig. 317.

In ganoids and teleosts there are additional devices for protecting the delicate gills, besides the opercular lid. Along the posterior and ventral margins of the operculum beyond the part stiffened by the flat opercular bones, there is sometimes a bordering flap, which, supported by fanlike skeletal elements, the *brancheostegal rays*, helps in controlling the passage of water out of the branchial cavity.

On the inner pharyngeal side of the gill slits also there are present in varying degree, series of stiff, comblike projections along the inner margins of the gill arches, the *gill rakers*. These structures not only shield the gills against contact with food that is being swallowed, but they also aid in directing it along the straight and narrow path in which it should go.

6. Dipnoian Gills

Of the three genera of living lungfishes, that are found respectively in Africa, Australia, and South America, *Protopterus* has six pairs of gill slits, *Neoceratodus*, five, and *Lepidosiren*, four. Spiracles are present in the embryos of these fishes, although not in the adults. In addition to pharyngeal gills, which are common to this group, supplementary *external* gill filaments are present in the larva of *Lepidosiren*, and throughout life in *Protopterus*.

7. Amphibian Gills

The epidermal gills of amphibians are external in character, being attached as capillary detours (Fig. 277, C), upon the vascular loops in such a way that the blood can go either directly around the vascular loops, or roundabout through the external gills (Fig. 318). This is unlike the arrangement of the internal gills of fishes, which offers no alternative for the circulating blood except to pass through the gills themselves.

Fig. 318.—Ventral view of the external gills and head blood vessels of a newt larva, *Triton*. These gills can be discarded without disastrous interference with the circulation, since they are not in the only possible path from heart to body. (From Haller, after Maurer.)

Unlike the internal entodermal gills they are not supported by a skeletal framework, and, although always present during the tadpole stages of amphibians, persist only in the perennibranchiate urodeles. Such external gills also occur in the larval forms of a few fishes, for example, in elasmobranchs and dipnoians generally, in the ganoids *Polypterus* and *Calamoichthys*, and the teleosts *Gymnarchus* and *Heterotis*.

The urodele amphibians have been separated into three groups, according to the character of their gills, as follows: (1) *Perennibranchiata*, retaining both gills and gill slits throughout life; (2) *Derotremata*, losing gills and all the gill slits except one pair; and (3) *Myctodera*, or true salamanders, having neither gills nor gill slits when adult. Although the perennibranchiates preserve throughout life their tadpole-like external gills and two or three pairs of gill slits, these pharyngeal openings are no longer useful for their original purpose, since the water of respiration does not pass through the pharynx. Instead, a fresh supply of oxygen is brought into contact with the gill filaments as the gills wave to and fro in the water, by means of muscles attached

to the base of each gill. Five pairs of gill pouches form embryologically in the pharyngeal cavity, but the first and fifth no longer break through.

In derotremes only the gill slit between the third and fourth gill arches becomes complete, while the external gills vanish during larval life.

The myctodere salamanders, as well as frogs and toads, have no gill slits, although embryonic gill pouches and gill clefts are formed. The temporary external gills of these forms are sacrificed with the development of pulmonary and cutaneous respiration.

Fig. 319.—External leaflike gills of a larval apodan, *Cæcilia compressicaudata*. (After P. & F. Sarasin.)

The external gills of anuran tadpoles become enclosed during metamorphosis by a fold of the skin without skeletal support. The protective peribranchiate chamber thus formed usually has a single opening to the outside, more rarely two, as in *Pipa* and *Xenopus*, corresponding physiologically to the atrial pore in the peribranchial chamber of amphioxus.

The larval external gills of *Cæcilia compressicauda*, one of the tropical limbless Amphibia, are exceptional, being peculiar leaflike structures with a relatively large respiratory surface (Fig. 319).

8. Gill Structures in Land Vertebrates

The persistence of branchial remains in land forms, that have no use for gills even in embryonic life, is striking evidence of the common ancestry of all vertebrates.

Although gills are never present in reptiles, birds, or mammals, there are five pairs of gill pouches and gill clefts in reptiles, and four pairs in birds and mammals, that do not normally break through as gill slits, with the exception of the hyomandibular pair which becomes the Eustachian tube and the cavity of the

middle ear. Occasionally a cervical fistula is seen in man, which is an abnormality that finds a reasonable explanation as an ancestral gill slit.

The further fate of the branchial arches will be considered in Chap. XVII, on the Skeleton.

III. SWIM BLADDER

The swim bladder of most fishes is a derivative of the anterior end of the digestive tube. If not primarily respiratory in function, it is at least found in suspicious intimacy with respiratory organs.

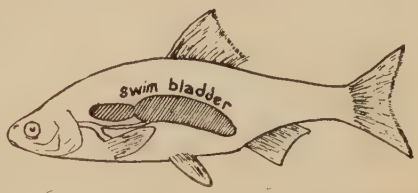


FIG. 320.—Location of the swim bladder. (After Hesse.)

It is located dorsally in the body cavity just outside the peritoneum (Fig. 320), under the vertebral column, and is primarily a single elongated structure, although it may be bifurcated or paired, as for example in the swellfish, *Sphæroides*, the curious headfish, *Mola*, and the sea robin, *Prionotus* among teleosts, and *Polypterus* and *Calamoichthys* among ganoids.

In amphioxus, cyclostomes, elasmobranchs, and a few of the higher fishes, particularly the bottom feeders and deep sea forms, it is absent. The flatfishes (Pleuronectidæ) possess a swim bladder only in early life during the period when they maintain a vertical position. As they tip over on one side in the course of development and assume their lazy adult habit of life, the swim bladder degenerates.

Fishes are classified into two groups in the adult, according to the character of the swim bladder, namely: the PHYSOSTOMI, having a *pneumatic duct* leading from the swim bladder to the alimentary tract; and the PHYSOCLISTI, having the duct closed or atrophied. To the first group belong the bony ganoids, the Dipnoi, and the soft-rayed teleosts. In the latter group are included all the spiny-rayed fishes.

The pickerel, *Esox*, represents a simple type of physostomous fish having a single sac for a swim bladder, with a pneumatic duct at the anterior end opening into the esophagus (Fig. 321, A). In the carps (Cyprinidæ, Fig. 321, B), a secondary *anterior*

chamber grows forward from the primary chamber which with its duct now becomes the *posterior chamber.*

In physoclistous fishes, with the degeneration of the pneumatic duct, the swim bladder becomes a closed sac having two chambers separated by a partition through which there is a sphincter-like opening, regulated in size by both circular and radiating muscles similar to those in the iris of the eye. The posterior chamber is formed by the enlargement of the pneumatic duct, which is no longer needed for its original function. This is quite apparent in the eel, *Anguilla*, a physostomous fish on the verge of becoming physoclistous, in which the duct is caught in the very act of enlargement into a separate chamber (Fig. 321, C).

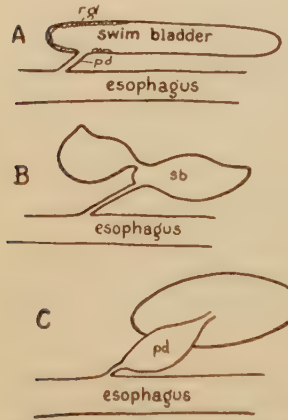


FIG. 321.—Diagrams of swim bladders. *A*, pickerel; *B*, carp; *C*, eel. *p.d.*, pneumatic duct; *r.gl.*, red gland; *s.b.*, swim bladder. The eel shows the posterior chamber forming by the enlargement of the pneumatic duct. (After Tracy.)

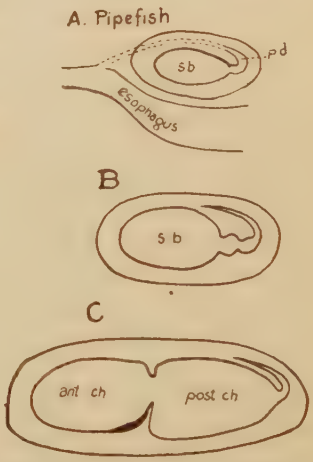


FIG. 322.—Diagrams to show the formation of the posterior chamber of the swim bladder from the pneumatic duct in the pipefish, *Siphostoma*. *A*, at the time of the release of the larva from the brood sac; *B*, stump of pneumatic duct growing backward to form U-shaped tube; *C*, pneumatic duct expanded to form posterior chamber. *s.b.*, swim bladder; *p.d.*, pneumatic duct; *ant. ch.*, anterior chamber; *post. ch.*, posterior chamber. (After Tracy.)

The formation of the posterior chamber by the enlargement of the pneumatic duct has been clearly indicated by Tracy in a series of diagrams, showing stages in the development of the swim bladder in the pipefish, *Siphostoma* (Fig. 322). The man-

ner in which the anterior chamber is produced by the forward growth of the budding swim bladder has also been demonstrated by Tracy, in the early stages of the toadfish, *Opsanus* (Fig. 323), which later develops a typical closed swim bladder, with the same three histological layers of tissue that characterize the alimentary tract from which it was derived. (Shown in section in Fig. 323, f.)

An important modification in the epithelial tissue lining the projecting anterior end of the swim bladder, results in a structure which is unique among animal tissues. This is the so-called *red gland*, which produces free oxygen (O_2) by the breaking down of red blood corpuscles that are brought into close contact with

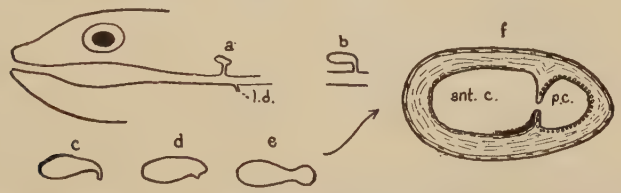


FIG. 323.—Diagrams of the early stages in the formation of the closed swim bladder in the toadfish, *Opsanus*. *l.d.*, liver duct; *ant.c.*, anterior chamber; *p.c.*, posterior chamber. (After Tracy.)

secreting epithelial cells. No other "gland" is capable of isolating pure molecular oxygen. As Tower has demonstrated, this oxygen constitutes a large part of the gas that distends the swim bladder.

Excess gas produced by the red gland escapes through the pneumatic duct in all physostomous fishes. Since the two-chambered swim bladders of physoclistous fishes have the red gland located in the anterior chamber, the mechanism for the removal of excess gas is of necessity different from that in fishes with a pneumatic duct. The posterior chamber is lined with a capillary network, the *rete mirabile*, through which the excess of gas generated in the red gland is absorbed directly into the blood for removal through the gills. By enlarging the opening in the partition between the chambers, more gas is admitted to the posterior chamber for disposal through the blood, while by restricting it, the gas is retained. In this way the degree of distention of the swim bladder is automatically regulated by the interaction of the red gland and the rete mirabile.

A further modification of the closed swim bladder sometimes occurs in the posterior chamber which, with the rete mirabile, becomes flattened almost to obliteration into a structure called the *oval*, as in the squeteague, *Cynoscion* (Fig. 324).

There are various uses for the swim bladder in fishes. Primarily it is a *hydrostatic organ* or "float," for the purpose of maintaining a certain level in water without muscular effort. When its gaseous content is increased, the fish rises to higher levels, or if diminished, sinks deeper in the water. By shifting the volume of gas from one end of the swim bladder to the other through muscular compression, changes in the center of balance in the body also occur, which enable the fish to make a variety of movements easily at the same level.

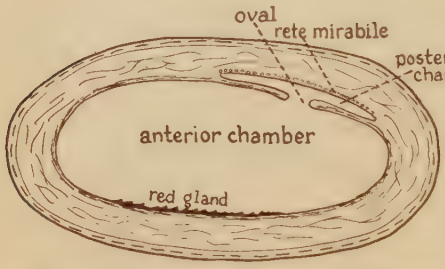


FIG. 324.—Closed swim bladder of squeteague, *Cynoscion*, showing oval, rete mirabile, and red gland. (After Tracy.)

In some fishes, particularly Siluroids, Cyprinoids, and Gymnoti, anterior prolongations of the swim bladder are found that come into intimate relation with the inner ear through a chain of bones, forming the so-called *Weber's organ*. By means of this apparatus, variations in the distension of the swim bladder are conveyed to the inner ear. This device probably acts as a regulatory sense organ, either after the fashion of a manometer or barometer. Whether Weber's organ aids in any way as an organ of hearing, has not been definitely determined.

Another use for the swim bladder is the function of *respiration*, for which reason its description is included in the present chapter. This function applies particularly to the lungfishes, in which the swim bladder becomes alveolar inside like the lungs of amphibians and the lower reptiles, being usually paired, as well as taking on all the essential features of simple lungs. It even derives, after the fashion of true lungs, a supply of venous blood from the last pair of vascular loops, whereas the typical hydrostatic swim bladder receives arterial blood only and gives off venous blood. Apparently the swim bladder of lungfishes

is, therefore, a more efficient breathing organ than the primitive lungs of the perennibranchiate urodeles.

A third incidental use of the swim bladder is the *production of sound*. Drumfishes (Sciænidæ), "grunters" (Hæmulidæ), and a few other forms, such as the sea robin, *Prionotus*, and the toadfish, *Opsanus*, are exceptional noise producers among the otherwise mostly silent brotherhood of fishes. According to Tower, who has carefully investigated the matter, the chief cause of the drumming noise in drumfishes is the contraction of a drumming muscle, *musculus sonificus* (Fig. 325), which being superficially attached to the swim bladder, "produces a vibration of the abdominal walls and organs, and especially of the swim bladder." D. S. Jordan says that the "grunting" of the Hæmulidæ is caused "by forcing air from part to part of the complex swim bladder."

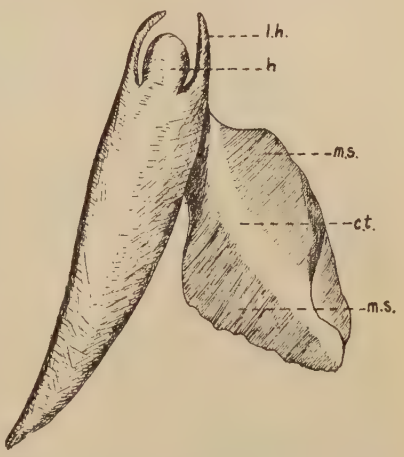


Fig. 325.—Swim bladder of male squeteague, *Cynoscion*. The double *musculus sonificus*, *m.s.*, is shown laterally displaced. *h.*, head; *l.h.*, lateral horn; *c.t.*, central tendon of *musculus sonificus*, which lies free in the mid-dorsal line just above the swim bladder, between it and the kidneys. The double *musculus sonificus* is inserted laterally in the common fascia of the *rectus abdominis*, and by its contraction in connection with the distended swim bladder, gives rise to the drumming sound. (After Tower.)

IV. LUNGS

1. General Plan

Lungs are the typical breathing organs of the higher vertebrates. Physiologically they represent an apparatus interposed between the two parts of a double heart, in which air and blood are brought together. Morphologically they consist of a much elaborated respiratory surface of maximum exposure within a minimum space, together with a system of non-collapsible passage-ways for admitting air from the outside to pass over these respiratory surfaces in intimate juxtaposition with capillaries.

The passage-ways begin either with the *nasal chamber* or *oral*

cavity, leading through the *pharynx* to the *trachea*, *bronchi*, and *bronchioles*, eventually reaching the innumerable terminal *alveolar sacs* that constitute the true respiratory part where the gaseous exchange of respiration is effected.

The whole lung apparatus in structure somewhat resembles a compound sebaceous gland, in which the air passages correspond to the ducts of the gland, and the respiratory mechanism proper to the glandular cells.

It is estimated that in man the respiratory alveolar surface enmeshed in capillaries, makes a total expanse a hundred times the area of the entire skin, or, if inflated into a single sac, that would form a balloon ten feet in diameter, yet this extensive structure is packed away in a relatively small space, the contour of which is determined largely by neighboring organs and the general body form.

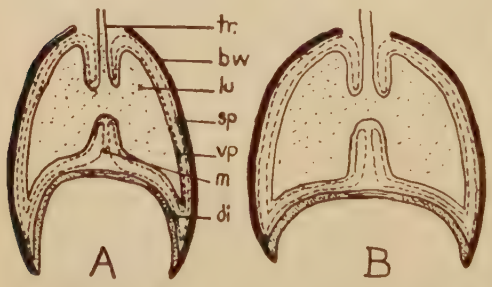


FIG. 326.—The lungs within the thoracic cavity. *A*, air expired by raised diaphragm and compressed ribs; *B*, air drawn in by lowered diaphragm and expanded ribs. *bw*, body wall; *di*, diaphragm; *lu*, lung; *m*, mediastinum; *sp*, somatic pleura; *tr*, trachea; *vp*, visceral pleura. (After Mollier.)

The alveoli, in contact with the capillaries, are lined with thin pavement endothelium, but the trachea, bronchi, and in part the bronchioles leading to the alveoli, are lined with columnar ciliated cells, the activity of which, so long as they remain moist, tends to keep the air passages free from dust and other foreign intrusions.

The lungs as a whole are highly elastic and, although encapsuled in a double pleural sac in the higher vertebrates, are freely movable within the sac, except at their point of attachment near the base of the bronchi (Fig. 326).

The whole apparatus might be compared to a luxuriant tree, entirely hollow in all its parts, that has been pulled up by the roots and crowded head first into a bag. The root region corresponds to the nasal chamber, the oral cavity and the pharynx; the main trunk to the trachea; the larger branches to the bronchi that subdivide into innumerable lesser branches and twigs, the

bronchioles, terminating in the leafy foliage, or alveoli, crowded together so as to occupy all available space within the enveloping sac, or pleura.

2. Air Passages

A. Nasal Chamber and Pharynx

The entrance to the pulmonary system is usually through the nasal chamber (Fig. 245), although in higher vertebrates the oral cavity may also serve in an emergency as an entrance. The surface of the nasal chamber, or nasopharynx, is covered with mucous membrane and supplied with capillaries, thus providing moisture and a certain degree of warmth for the incoming air. A moist surface is further insured by the fact that lacrimal canals from constantly operating tear glands, drain into this chamber.

The walls of the nasal chamber are variously modified in different vertebrates by scroll-like turbinate bones, which not only increase the moist vascular surface, but also prevent easy entrance of undesirable objects, by making the passage-way tortuous. This latter purpose is also furthered by a forest, more or less dense, of outward-projecting hairs, guarding the entrances of the nasal chamber, or nostrils.

B. Trachea

From the nasopharynx air passes back through the oropharynx to the laryngopharynx, where it crosses the pathway of food on the way to the esophagus, thence entering the trachea through the opening of the *glottis*.

The trachea, or "windpipe," is very short in anurans, whose lungs are placed far anterior in the body cavity. It is somewhat longer but still insignificant in the urodeles. In lizards it is relatively shorter than in other reptiles, although unmistakably present, while in turtles and crocodiles it is frequently so long that it becomes convoluted or even spiral in form. The lengthened trachea in the chelonians is an accommodation to the accordeon-like movements of the head and neck.

Birds with long necks are, of course, provided with a long trachea, but frequently the trachea is longer even than the neck itself so that it cannot remain straight but loops about. In swans these extra loops are stored within the hollow breastbone (Fig. 327), while in some birds they lie coiled under the skin, or may even extend into the body cavity.

Usually the windpipe is nearly cylindrical, but sometimes, as in the little vocal wall lizards, or "geckos," and also certain ducks, it may show a bulblike enlargement.

In mammals the trachea is practically straight, with a length dependent upon that of the neck, except in the three-toed sloth, *Bradypus*, which has the trachea so elongated that it extends down to the diaphragm and back before entering the lungs.

At all times the elastic walls of the trachea are kept mechanically distended for the passage of air by encircling rings of cartilage, resembling the rings of metal embedded in a garden hose to give

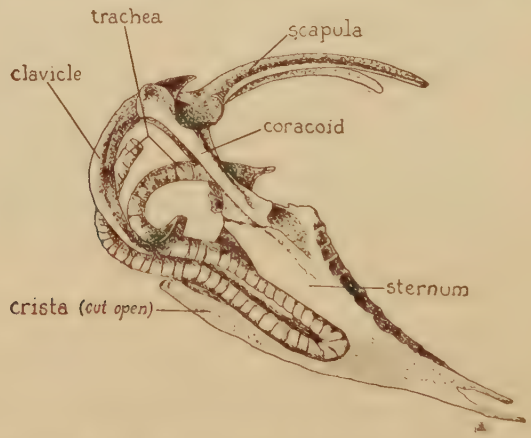


FIG. 327.—Trachea of swan, embedded in sternum. (After Schimkewitsch.)

it flexibility and durability. In the case of mammals these skeletal tracheal rings are usually incomplete dorsally, that is, on the side liable to press against the digestive tube, thus minimizing the corduroy-road effect that might otherwise be produced upon them by a bolus of food passing down the neighboring esophagus.

Among reptiles, birds, and pinnipede mammals, the tracheal rings are entire, while cetaceans present the unusual case of ventrally incomplete rings.

Camels and giraffes are noteworthy in having upwards of 100 separate tracheal rings, and whales and sea cows by having these skeletal structures spirally arranged. Although usually of hyaline cartilage, the tracheal rings become bony in the python, *Agama*, as also in many birds.

C. Bronchi

The trachea usually branches into two bronchi, that resemble it with the exception of being smaller in size and having weaker skeletal rings. There are three bronchi in certain ruminants, pigs, and whales, whereas in most snakes, with the degeneration of one of the lungs as an accommodation to the extraordinarily elongated shape of the body, there remains only one bronchus.

D. Bronchioles

The bronchioles, which continue and multiply the air passages from the bronchi, have neither cartilage supports in their walls nor mucous cells in their linings. The terminal bronchioles are also without cilia, and serve simply as ducts opening into the ultimate air chambers, or alveoli, in which respiration occurs.

In mammals generally the bronchioles arise like the twigs of a tree and diverge from each other, but in crocodiles and birds they run together, forming intercommunicating loops, from the sides of which the alveoli are given off.

E. Alveoli

The alveolar sacs are hemispherical enlargements with exceedingly thin, delicate, highly elastic walls, over the outside of which, like vines over a trellis, extends a maze of capillaries (Fig. 328). It is estimated that in a pair of human lungs there may be more than six million of these tiny chambers, all in ultimate communication with the outside atmosphere through the air passages.

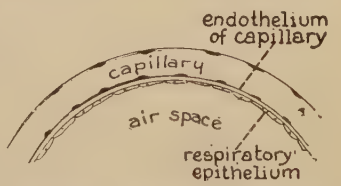


Fig. 328.—Diagram of partitions between blood and air in an alveolus.

The amount of air admitted to the separate alveoli is automatically regulated by means of nerve endings, whose headquarters are located in the medulla of the brain. They insert into tiny cuffs of circular muscle fibers around the walls of the innumerable bronchioles, causing them to constrict or relax, as occasion demands.

3. Phylogeny

The phylogeny, or comparative anatomy of vertebrate lungs, is a story of internal modification for the increase and efficiency of respiratory surface, and also for adaptation to the shape of the

body. The bestowal of lungs, for example, within the body of a squat toad, a lithe cat, a capacious cow, a box turtle, or an elongated snake, presents in each instance a different problem.

A. Dipnoi

A transition from the swim bladder to true lungs is found in the Dipnoi. During the æstivation of these lungfishes the gills are not used for respiratory purposes but, instead, the pulmonary arteries bring venous or "impure blood" to the swim bladder, which then functions as a lung, although both trachea and bronchi are wanting.

In *Neoceratodus*, the lung is a single wide sac, resembling the swim bladder of physostomous fishes, but in *Protopterus* and *Lepidosiren*, the sac is double, its inner surface being increased somewhat by its coarse, spongy, alveolar structure.

B. Amphibia

Amphibians in general carry on the pulmonary plan of the Dipnoi, although the lungs of certain perennibranchiate urodeles are less elaborated than those of the lungfishes. The lungs of *Necturus*, for example (Fig. 329), are two long simple sacs, enmeshed on the outside by arterial and venous capillaries and opening directly through a slitlike glottis without the intervention of trachea or bronchi, or the inner surface increased by folds. The whole apparatus resembles a pair of enlarged, elongated alveolar sacs.

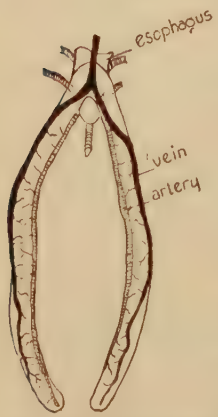


Fig. 329.—The blood vessels of the lung of *Necturus*. *e*, esophagus; *p.a*, pulmonary artery; *p.v*, pulmonary vein. (After Miller.)

Amphiuma goes a step further, in that the proximal half of each lung has the inside surface considerably increased by the development of folds.

Owing to their body form, frogs and toads have more spherical lungs than salamanders. The folds within a frog's lungs extend from the inner wall in such a way as to divide the entire cavity into stall-like spaces, all opening freely into a common central cavity. The walls within the "stalls" become further increased by minor folds, each of which carries its individual capillary supply (Fig. 330), whereas in toads the stalls become more definitely shut off from the central cavity of the lung by expansions

along the inner margins of the major partitions, so that a secondary internal wall is elaborated, that is perforated on all sides with openings between the central cavity and the air chambers, or "stalls."

The very primitive tracheal and bronchial tubes of amphibians enter the lungs at the extreme anterior end. With an increased development of the anterior part of the lungs, the bronchi come to enter laterally in higher forms.

As a result of a migratory invasion into the body cavity, the lungs of amphibians are invested by a single layer of peritoneum,

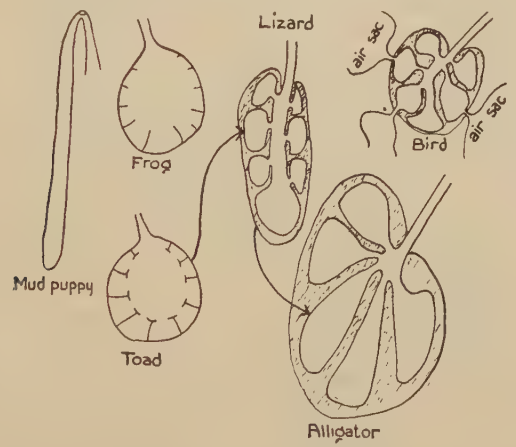


FIG. 330.—Diagrams to show the evolution of lung structure. The plan of a lizard's lung may be regarded as like a cluster of toads' lungs, and in turn the alligator's lung, as composed of several lizards' lungs. The air sacs of the bird extend beyond the lung itself but are in communication with it.

which was pushed ahead of them into the body cavity during development. They do not, therefore, have a pleural cavity of their own, but instead lie freely in the common body cavity.

Usually the left lung in amphibians is larger than the right one, but in tropical legless forms, Gymnophiona or Apoda, the reverse is true, as the left lung is rudimentary. Some salamanders, for example, *Eurycea* and *Salamandrina*, are lungless.

C. Reptiles

Reptilian lungs are also abdominal in position but much sacculated within, the trachea and bronchi being developed into definite structures.

The primitive New Zealand lizard, *Sphenodon*, has spongy lungs that might be compared to a series of toadlike lungs, opening into a common passage, or *atrium* (Fig. 330), while the lungs of crocodiles go a step further in elaboration, corresponding structurally to a bouquet of *Sphenodon* lungs placed together, the atria of which open into a common bronchus (Fig. 330).

Fig. 331. -Lungs of *Chameleon*, showing supplementary air sacs. (After Hilzheimer.)

In snakes the left lung usually becomes aborted, only the right lung remaining to occupy the narrow quarters that are available. Boa constrictors and pythons are the most ancestral in this respect, having both lungs present, with the left one somewhat shorter than the right.

The different regions of the long single lung of the snake are unequally elaborated, recapitulating from tip to entrance the early phylogeny of vertebrate lungs. The distal tip is a smooth sac, like the lung of *Necturus*, but advancing towards the proximal or anterior end, there appears a gradual evolution of internal folds, at first resembling the lungs of *Amphiuma*, and later the chambered structure of the lungs of frogs and toads. Finally, at the base, these chambers become compounded and open into an atrium, which suggests the degree of complexity arrived at in the lung of *Sphenodon*.

Certain lizards, particularly *Chameleon* (Fig. 331), have peculiar lungs with saclike diverticula, which enable them to swell up to some extent, a device used perhaps to frighten their enemies. The inflated lungs of sea turtles, on the contrary, probably serve as floats, or life preservers, in maintaining a position at the surface of the water.

D. Birds

The lungs of all modern birds are highly modified by the presence of supplementary air sacs, *cellulæ aëreæ*, which facilitate the circulation of air through the lungs, but in themselves are not directly respiratory in function. The bronchioles, instead of ending blindly in alveolar sacs, form a system of communicating loops, with alveoli on the sides, opening eventually into the reservoir-like air sacs (Fig. 332). It is possible, therefore, for the air to be

drawn back and forth *entirely through* the alveolar region of the lungs, with gaseous exchange occurring both on the way through the lungs to the air sacs as well as on the return.

Embryologically, air sacs sprout out from the ventral surface of the lungs at various points and extend into the body cavity,

FIG. 332.—The injected air sacs of a pigeon, represented in black, showing how completely they occupy all available spaces. The lungs are shown by horizontal lines behind the ribs. (After Müller.)

occupying spaces between the viscera; between the muscles, supplanting connective and fatty tissues; beneath the skin (in pelicans); between and around the joints of the cervical vertebræ; and penetrating even into the pneumatic cavities of hollow bones. The primitive *Apteryx* of New Zealand, alone among birds, has much reduced air sacs that do not enter the bones or penetrate the transverse septum to extend into the body cavity.

Unlike the alveolar sacs of the lungs, the walls of the air sacs are not supplied to any great extent with a capillary network, and consequently are not directly respiratory in function. They have, however, at least six different uses, acting as bellows, balloons, ballast, friction pads, heat retainers, and reservoirs.

Since much of the elasticity of a bird's lung is lost by being anchored fast to the dorsal wall of the thoracic basket, a mechanical aid for effecting an efficient circulation of air through the lungs becomes all the more necessary. Such a mechanism is supplied by the air sacs acting as bellows. In the capacity of balloons, the air sacs when inflated cause the specific gravity of the bird to be materially lessened. Without them it would require considerably more muscular effort to sustain a body heavier than air in suspension for considerable periods of time. Possibly inflated air sacs may also by their turgor, mechanically aid in maintaining the wings in an extended position during soaring or volplaning. As ballast, the arrangement of the air sacs is such that a proper center of gravity is established for balanced flight, so that equilibrium is easily maintained. The insertion of air sacs between the muscles lessens friction, thereby giving flexibility and grace to the movement of birds, and when filled with warm, moist air, they help to maintain and regulate the body temperature. In the absence of evaporating sweat, the skin of birds is of little service for this purpose. As containers for reserve air the air sacs are undoubtedly useful. The muscular mechanism by which a resting bird causes air to enter the lungs, involves the elevation and depression of the breastbone through the activity of the intercostal muscles. It is necessary, however, for the breastbone to remain firm during flight, to insure anchorage of the powerful flying muscles, while the intercostal respiratory muscles are held in tension and are, for the time being, not pumping fresh air into the lungs. Therefore, an internal reservoir of air is indispensable, while the flying muscles which ventilate the lungs by acting upon the air sacs as bellows, also control respiratory movements during flight. The more rapid the flight, the greater is the automatic supply of air drawn through the lungs to and from the pneumatic chambers. Violent action in mammals interferes with respiration, but in birds it enhances it. This is why fast-flying birds do not "get out of breath," or probably suffer from "mountain sickness" in the air of high altitudes, because the necessarily increased wing strokes bring in a compen-

satory supply of rarified air. The frigate bird, *Fregata*, that easily maintains a rate of 100 miles an hour, has about the best development of air sacs to be found in any bird.

The pneumatic diverticula of the lungs of *Chameleon*, already mentioned (Fig. 331), and those of certain other lizards, may perhaps be regarded as prophetic of the air sacs of birds.

E. Mammals

The lungs of mammals are usually characterized in at least two ways, first, by being subdivided externally into two lobes, and secondly, by showing some degree of asymmetry in accommodation to surrounding organs.

When asymmetry occurs the lobes are more numerous on the right than on the left side. Thus, in man (Fig. 333), there are three lobes in the right lung and two in the left. The uppermost odd lobe of the right lung lies behind the right pulmonary artery, while the absence of a corresponding lobe on the left side permits the presence of the large left aortic arch.

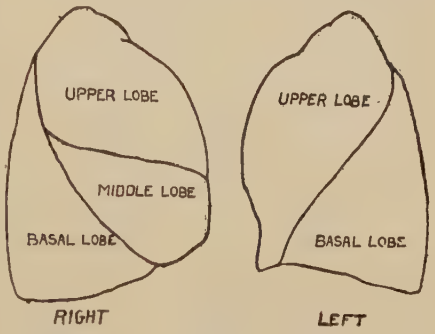


Fig. 333.—Lobes of human lung. Outline of the outer, or costal, surface. (After Cunningham.)

Certain mammals, as for example, Cetacea, Sirenia, Proboscidea, Hyracoidea, and most perissodactyl Ungulata, resemble other vertebrates in the absence of pulmonary lobes, while Monotremata are transitional, since they possess lobes only in the right lung.

The relative size of the right human lung as compared with the left, is about eleven to ten, for, although the right lung is slightly shorter, it is somewhat larger in area.

The lungs of whales, which are located rather posteriorly in the hulls of these sea-going leviathians, are probably hydrostatic as well as respiratory in function.

4. Pleural Envelopes

The lungs of higher vertebrates are enclosed in compartments called *pleural cavities*, separated from the body cavity which is the general storehouse of the internal organs. The establish-

ment in mammals of exclusive chambers for the lungs, has been a gradual evolutionary process. The primitive lungs of amphibians push down into the body cavity, carrying with them a thin covering of serosa continuous with the peritoneum that lines this common cavity, but without the formation of independent pleural chambers. In reptiles, along with the formation of a *transverse septum* through the invasion of peritoneal folds, and the assurance of privacy for the heart by the shutting off of a pericardial chamber, there is formed around the lungs a second envelope derived from the peritoneal serosa, that constitutes the outer, or *parietal,* wall of the pleural cavity (Fig. 326). The inner, or *visceral,* wall is the original derivative of the peritoneum already mentioned and this intimately invests the lungs like a tight-fitting garment. The space between the parietal and visceral walls, the pleural cavity, is filled with a serous, lubricating fluid, that allows freedom of movement on the part of the extensible lungs within the pleural space.

5. Origin of the Lungs

The lungs, like the swim bladder, probably come from rudimentary gill pouches. The swim bladder is a dorsal outgrowth

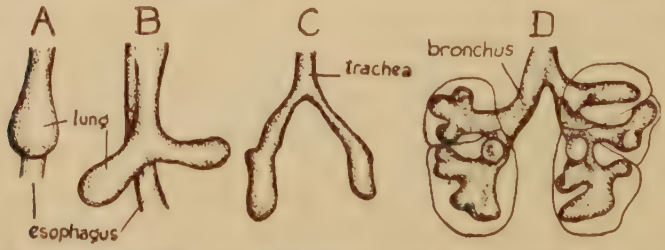


FIG. 334.—Early stages in the development of lungs, trachea, and bronchi of human embryos. *A*, 4 mm. embryo; *B*, 5 mm. embryo; *C*, 7 mm. embryo; *D*, 9 mm. embryo. (From Arey. *A,B,C,* after Prentiss; *D,* after Merkel.)

from the floor of the foregut, and the first evidence of lungs in man, which may be seen about the third week of fetal life, is a ventral groove in the floor of the same region. As this groove pushes deeper down, it forms a single bud that soon becomes a bilobed sac, representing the future lungs (Fig. 334). Soon after a common stem or duct is formed as the result of the further extension of the lung sacs. This is the trachea, whose ap-

pearance is followed by branching bronchi, and last of all, by the elaboration of subdivisions within the lung sacs, and the establishment of the alveoli.

During the differentiation of the lung sacs the entodermal lining invades the surrounding mesoderm, as shown by Moser in a series of illuminating diagrams (Fig. 335), with the end result that a maximum surface of respiratory entodermal tissue is brought into intimate contact, back to back, with vascular, mesodermal tissue carrying blood-filled capillaries.

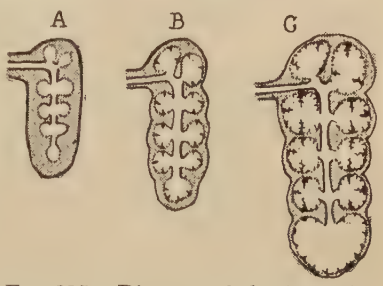


Fig. 335.—Diagram of the formation of the lungs in turtles. *A*, intrapulmonary bronchus, with several primary alveolar chambers invading the surrounding mesoderm; *B*, intermediate stage; *C*, the adult condition. The chambers have become subdivided into alveoli by ingrowth of their walls. Mesoderm reduced to partitions between the chambers. (After Moser.)

Human lungs assume definite shape before the end of the third month, although they do not take on their respiratory function as long as the embryonic placenta is active, and are probably not entirely inflated for three or four days after birth. The alveoli are laid down by the seventh month and thereafter merely undergo enlargement.

V. VOICE APPARATUS

The emotions of animals are frequently expressed in various ways by characteristic noises. Male rabbits sound an alarm by pounding the ground with their hind feet, and bucks and bulls send forth a resounding challenge by stamping their front hoofs. Rattlesnakes shake their caudal castanets, and many stridulating animals, particularly armored insects, express themselves audibly by rubbing hard parts together.

Among vertebrates that produce a distinctive noise, the voice apparatus is generally a wind instrument, and consequently is a direct part of the respiratory system.

The majority of vertebrates are dumb. Fishes, which outnumber all other vertebrates in species as well as in individuals, have only a few representatives, such as drumfishes and "grunters," which break over the piscine vow of silence.

Amphibia, excluding the musical Anura, are practically voiceless, and reptiles also, if a few unusual cases, such as hissing snakes, gutteral geckos, and bellowing bull alligators are omitted, are prevailingly silent.

Some moralist has pointed out the fact that probably the first vocal words which were spoken on this earth were the words "work, work, work" of the croaking frogs. It should also be noted that the frogs themselves, like many other givers of advice, pay no heed to their own exhortations.

Birds are notably vociferous as a rule, but there are numerous species, such as stalking ostriches and stately storks that preserve a dignified silence, while it is a curious fact that among mammals the gigantic whales have less voice than tiny mice.

The words in common use to describe sounds produced by mammals indicate a wide variety of distinctive "voices," with corresponding necessary diversity in the wind instruments involved. For example, the horse "whinnies"; the cow "moos"; the donkey "brays"; the pig "squeals"; the sheep "bleats"; the elephant "trumpets"; the porcupine "grunts"; the lion "roars"; the cat "purrs"; the wolf "howls"; the dog "barks"; the rat "squeaks"; the monkey "chatters"; the lemur "wails"; and some men "sing."

Since most voices are dependent upon the expulsion of air from the lungs, the vocal apparatus, or *larynx*, is advantageously located around the *glottis*, that is, the opening of the trachea. Different sounds are produced by modifying the shape of the aperture through which the expelled air escapes. The cartilages, membranes and muscles of the larynx constitute a mechanism for effecting this result. The mouth cavity also, particularly in man with his pliable cheeks and flexible tongue, aids greatly in altering the character of the chamber through which the column of air from the lungs is forced. This can be easily demonstrated by pronouncing the vowels, A, E, I, O, U, in slow succession and mentally noting the changes that result mean-

FIG. 336.—Section of the parts concerned in phonation, and the changes in form involved in sounding the vowels, *A*,*I*,*U*. *T*, tongue; *e*, epigiottis; *h*, hyoid bone; *1*, thyreoid cartilage; *2*,*3*, cricoid cartilage. (After Landois and Stirling.)

while in the position of lips, tongue, and cheeks, and the consequent alteration in the contour of the mouth cavity while executing these distinctive sounds (Fig. 336). In this connection it is a suggestive fact that the evolution of voice has a close dependence upon emergence from water to life in air.

1. Amphibians

There is no true larynx in fishes but in the voiceless salamanders the larynx consists of two tiny triangular guardian cartilages, *lateral cartilages* (Fig. 337), embedded one on either side of the glottis. In some cases when there is trachea enough to permit, as in *Siren*, for example, there are additional fragmentary cartilaginous rings below the laterals. These prophetic cartilages of the urodeles become developed into elongated laryngeal cartilages in the muscial frogs, toads, and hylas. The "brek-ek-ek-kex, ko-ax, ko-ax," of Aristophanes' famous frogs, imitated in one of the modern college "yells," is a virile characteristic bit of vocalization familiar to every one whose experiences include a frog pond in springtime.

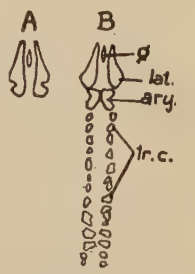


FIG. 337.—Laryngeal cartilages of urodeles. *A*, *Necturus; B*, *Siren*. *ary.*, arytænoids; *lat.*, lateral cartilages; *g.*, glottis; *tr.c.*, tracheal cartilages. (After Wiedersheim.)

The mechanism which produces these haunting nocturnes, consists of a pair of lateral, or *arytænoid*, cartilages, and in addition, of a new cartilage, the *cricoid*, which is an elaboration of the first tracheal ring or rings (Fig. 338). Dilator and adductor muscles operate these skeletal elements.

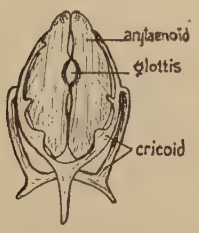


FIG. 338.—Voice apparatus of a frog. (After Wiedersheim.)

The larynx is surrounded by a small laryngotracheal chamber, while two folds, the *vocal cords*, which lie parallel with the slit-like glottis, are present on the inner wall of this chamber. The Anura, especially the males of the species, have besides, internal *vocal sacs* in the throat region, which, when inflated, are apparent externally. These serve as chambers of resonance for increasing the carrying quality of their vocalizations. There is a single median vocal sac in all Hylas (Fig. 339), as well as in the toad, *Bufo*, while two lateral sacs

show at the shoulders of frogs, being especially pronounced in the male bullfrog, *Rana catesbiana*, when its twanging "jug-o'-rum" note is being broadcast. As a matter of fact the lungs of Anura are largely organs for producing sound after the manner of bagpipes, the respiratory function being taken over mostly by the skin, as is indicated by the cutaneous arteries, which exceed the pulmonary arteries in size.

FIG. 339.—*Hyla*, showing inflated resonance sac. (After Boulenger.)

2. Reptiles and Birds

Reptiles and birds have less larynx and more trachea than the Anura. Birds have evolved, in addition, a secondary larynx, called the *syrinx*, which is located at the lower end of the trachea at its junction with the bronchi, instead of around the glottis (Fig. 340). The position of this unique voice box is in line with the extreme structural adaptations of birds, whereby all possible weight is centralized for purposes of equilibrium in flight.

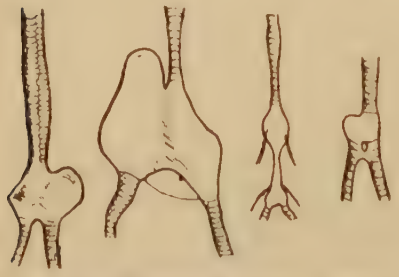


FIG. 340.—Different syringes. *A*, mallard; *B*, goosander; *C*, velvet scoter; *D*, eider duck. (After Pyecraft.)

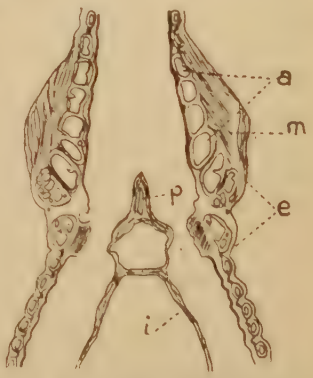


FIG. 341.—Longitudinal section through the syrinx of a thrush. *a*, "drum" formed from the last cartilaginous rings of the trachea; *m*, muscles; *e*, external elastic membrane forming the outer wall of the bronchi; *i*, internal elastic membrane; *p*, pessulus. (After Haecker.)

There are no vocal cords in birds, but instead a vibrating structure, the *pessulus* covered by the *membrana semilunaris* (Fig. 341), which acts somewhat like the reed in an organ pipe or a clarinet, to produce vibrations in the expired air. The cartilages of the syrinx are modifications of the tracheal and bronchial rings,

and are combined with intercartilages, membranous walls, and a variety of muscles. By means of this apparatus the bird is enabled to change the shape of the tracheobronchial chamber in which the pessulus vibrates, thus producing a variety of different sounds.

3. Mammals

The cartilages of the mammalian larynx include in addition to a pair of triangular *arytænoids* around the glottis, and a bandlike *cricoid* just below, a relatively large, quadrilateral, shieldshaped *thyreoid cartilage*, which in man forms the movable prominence in the neck known in academic circles as the *pomum Adami* and elsewhere as "Adam's apple."

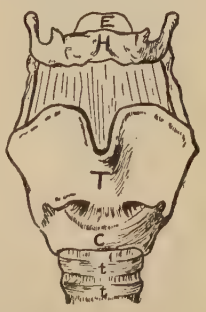


FIG. 342.—Front view of human larynx, *H*, hyoid bone with greater and lesser horns *E*, epiglottis; *T*, thyreoid cartilage ("Adam's apple"); *C*, cricoid cartilage; *t*, *t*, tracheal rings of the windpipe. (After Cunningham.)

The thyreoid cartilage is originally paired, as shown by the fact that in monotremes it is made up of two lateral plates instead of a single piece, and in all mammals is derived embryologically from the remains of paired branchial arches.

Still another structure developed in mammals is a cartilaginous lid above the glottis, called the *epiglottis*. This aids in closing off the tracheal tube from food that is passing down the esophagus, a process accomplished not so much by the closing down of the epiglottis as by the elevation of the tracheal tube to fit against the overhanging lid. That the larynx is temporarily elevated during the act of swallowing is easily demonstrated by placing the thumb and finger lightly against the "Adam's apple," at the same time imitating the transit of food by swallowing.

Furthermore, in mammals the horseshoe-shaped *hyoid bone*, situated above the glottis region, is made a part of the laryngeal complex by connecting ligaments. Certain minor laryngeal cartilages are present in human anatomy, for example, two minute rodlike *cuneiform cartilages of Wrisberg*, in the fold between the epiglottis and arytænoid; two small, conical nodules, the *cartilages of Santorini*, surmounting the apices of the arytænoids; and the *triticeous cartilages*, embedded in the ligaments connecting the

hyoid bone on either side with the thyreoid cartilage, and so-called because of a resemblance to grains of wheat (*Triticum*). The location and relationships of the various cartilages that make up the laryngeal voice box of man, are indicated in Fig. 342.

Fig. 343.—Vertical section of the larynx. *1*, posterior face of epiglottis; *2*, false vocal cord; *3*, true vocal cord; *4*, anterior part of cricoid; *5*, section of cricoid; *6*, cut surface of thyreoid cartilage; *7*, thyreo-hyoid membrane; *8*, thyreo-hyoid muscle; *9*, arytæno-epiglottic muscle; *10*, thyreo-arytænoid muscle; *11*, part of the thyreo-arytænoid muscle within true vocal cord; *12*, crico-thyreoid muscle; *13*, cavity of trachea. (After Testut.)

The vocal cords or bands, which reach their greatest differentiation in mammals, are two pairs of folds inside the larynx, one above the other, extending between the arytænoids and the thyreoid cartilage (Fig. 343). The upper pair are called "false," and the lower pair "true" vocal cords. They are made up of dense bands of elastic fibers covered over by mucous membrane, their position and tension being altered by means of accompanying muscles. During ordinary breathing they do not vibrate sufficiently to produce sound, but when desired the column of air that is forced over their surfaces may be modified through their activity into audible vibrations. In most cases sound is produced by the expiration of air over the vocal cords, but in exceptional instances, a familiar example of which is the "hee-haw" of the donkey, the air does vocal service both going in and coming out.

Between the true and false vocal cords is a groove or concavity, known as the *ventriculus laryngis* (*Morgagni*), which is particularly well developed in certain howling monkeys and vociferous apes, and has the capacity of swelling out on either side into resonance sacs that function much as do similar structures in the Anura, adding intensity to the sounds produced. Curiously, elephants are without false vocal cords while hippopotami have no others.

In young marsupials that remain attached to the nipples of the mother for protracted periods, by means of an automatic sphincter muscle, the larynx becomes so elongated that it extends up into the nasopharynx behind the soft palate, enabling these animals to breathe and to take in milk at the same time. This

device eliminates complications usually attendant upon the double traffic of air and food in the pharyngeal crossing of the ways.

Whales have an elongated larynx also, with the glottis enwrapped by the soft palate, an arrangement that mitigates some of the difficulties to which these most aberrant of all mammals are subjected by a nautical existence (Fig. 344).

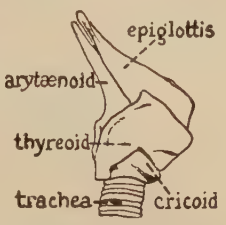


Fig. 344.—Larynx of *Ziphus cavirostris*. (After Gegenbaur.)

VI. DEVICES FOR SECURING AIR

The process of breathing demands more than a mechanism that simply allows blood and air to get within osmotic distance of each other, since there must also be present means for securing a continuous circulation of fresh air across the respiratory surfaces.

1. Fishes

In the case of submerged fishes, water charged with air entering either the mouth or the spiracles and passing out through the gill slits, is forwarded and directed in its course, not only by

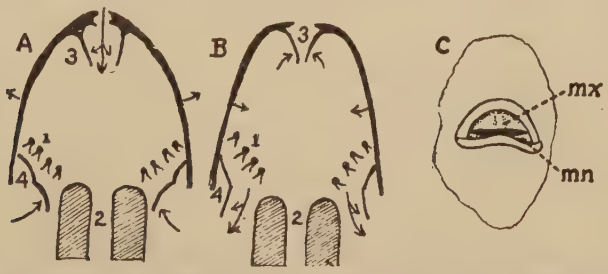


Fig. 345.—Diagram of mechanism for causing a respiratory current of water to pass over the gills in bony fishes. *A*, inspiration; *B*, expiration; *C*, anterior view of mouth; *1*, gills; *2*, esophagus; *3*, labial valves; *4*, branchiostegal valves; *mn*, mandible; *mx*, maxilla. (*A* and *B* after Dahlgren; *C*, after Kingsley.)

muscular movements, which alternately expand and contract the walls of the orobranchial chamber, but also by a system of valves that prevents the water from going the wrong way.

The anterior set of these valves are collapsible folds along the inner edge of the mouth opening, those on the upper edge being called *maxillary*, and those below, *mandibular*. They reach their greatest differentiation in teleost fishes which have no opercular

apparatus. The posterior, or *branchiostegal*, set of valves, are membranes along the free margins of the opercular flaps (Fig. 345). A freely moving current of water is produced in the following way. First, the mouth remains open as a narrow slit, while the anterior valves lie flat, or open, and the posterior valves close. Next the walls of the orobranchial chamber spread apart, thus pulling water into the mouth to occupy the increased space. Then the valves reverse, that is, the anterior ones close the slit-like mouth aperture, and the posterior ones open, while the walls of the orobranchial cavity squeeze together, forcing the water backward over the gills and out of the opercular openings.

In some teleosts, particularly those that feed upon microscopic plankton, the branchiostegal valves play the major rôle in this process, but in others, for example, the Percidæ and the Sciæridæ, the opercular flaps take the most prominent part.

Elasmobranch fishes, particularly the bottom-feeding skates and rays, substitute the spiracles for the mouth to a large extent, as an avenue for the intake of water.

2. Amphibians

Amphibians do not breathe through the open mouth, but instead they inspire through the nostrils and the *choanæ*, as the newly established passage-ways into the mouth cavity are called. They are not even able to exercise emergency breathing through the mouth, like mammals, for as long as the mouth remains open there is no way to compel the air to enter the lungs. *Necturus*, and other perennibranchiate urodeles, sometimes come to the surface of the water and gulp air through the mouth, which may be seen escaping soon in the form of bubbles through the gill slits, but it is doubtful if much of it reaches the lungs. This occasional air-gulping behavior on the part of these animals does not furnish fresh air for the external gills that hang outside the gill slits, since these, being supplied by muscles that cause them to wave back and forth, come into contact with a renewed supply of air dissolved in water.

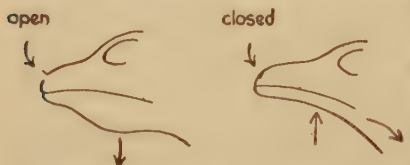


Fig. 346. — Breathing mechanism of a frog.

The intake of air in the frog, as a representative amphibian, is

accomplished by a pumplike combination of throat muscles and nostril valves, as shown in Fig. 346. It will be seen that when the nostril valves open and the throat muscles draw down, thus enlarging the cavity within, air is necessarily inhaled. With the closure of the nostril valves to prevent the escape of the mouthful of air the wrong way, and with the contraction of the throat muscles, the lungs inevitably become filled. The expiration of air is accomplished by means of the contraction of body muscles.

3. Reptiles

The problem of getting air into the lungs of reptiles is much like that in the case of amphibians, although an improvement is seen in the presence of ribs and rib muscles, which furnish a mechanical means of sucking in air that is not present in the practically ribless amphibians. This improvement is ineffective, however, in turtles, whose ribs form a boxlike armor of uncompromising rigidity. These animals still resort to the amphibian method of utilizing throat muscles and nostril valves, swallowing air by "working the throat." No doubt the accordeon-like movements of a turtle's head and neck aid in pumping air into the lungs, while the pectoral muscles, which are *inside the ribs* in these bizarre reptiles instead of outside as in all other vertebrates, are aided by the abdominal muscles to bring about the expulsion of air from the lungs. The usefulness of rib muscles in pumping air in and out of the lungs, is very apparent in snakes, lizards and alligators.

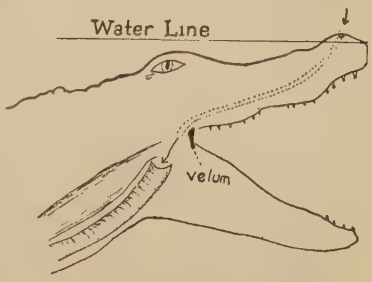


FIG. 347.—Diagram to show the choana (dotted) in an alligator. It leads to the trachea behind a flaplike *velum* in the back part of the mouth cavity, which enables the animal to breathe under water and at the same time to drown its prey held between the jaws, so long as the external nostrils are above the water line.

Alligators have an exceptionally elongated nasal passage-way with a *velum*, or curtain, that closes off the inner choanal opening from the mouth cavity. This makes it possible for them to breathe under water with the mouth open while drowning prey that is grasped between the cavernous jaws, when only the external nares are above the water line (Fig. 347).

4. Birds

So long as a bird is not in flight, it breathes by means of rib muscles after the manner of reptiles, chelonians excepted. When a bird flies, as already explained, the powerful pectoral muscles upon which flight depends, require and secure anchorage upon a *fixed* thoracic basket that does not change shape with every breath. The bellows-like air sacs, which are filled and emptied by the action of the flying muscles, furnish an effective means for irrigating the lungs of a flying bird with air, while the respiratory rib muscles remain temporarily rigid.

5. Mammals

In mammals both nasal and oral breathing are made possible by the migration of the glottis backward to a position in the posterior region of the throat. Nasal breathing, however, with the greater facilities thus provided for warming and moistening the inhaled air, and the added advantage of testing its quality by means of its passage over the sensitive olfactory surfaces in the nasal chamber, is the better and more favored method with mammals generally.

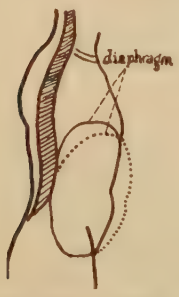


FIG. 348.—Abdominal contour of man in respiration. Solid line, inspiration; dotted line, expiration. (After Mollier.)

The outstanding advance in the breathing mechanism of mammals is furnished by the diaphragm. This is a muscular organ developed in part from the transverse septum, that separates the pleural and the pericardial chambers from the body cavity. It consists of a central tendinous component, from which extend radiating muscle fibers, derived in part from muscles of the body wall, the *transversus abdominis* and the *rectus abdominis*. The diaphragm is perforated by the dorsal aorta, esophagus, azygos vein, thoracic duct, vena cava, and vagus nerve, and is shaped when relaxed, somewhat like an arched vault (Fig. 348). As its radiating muscle fibers contract, the vault of the diaphragm lowers, thus tending to increase the space within the body cavity and thereby pulling in air. At the same time the viscera within the body cavity are crowded down so that the abdominal wall bulges out. The muscular opponents of the diaphragm are the strong walls of the abdomen.

In addition to abdominal breathing, mammals also utilize the reptilian method of rib muscles to enlarge the thoracic cavity and thus inspire air. The ribs are bent, like jointed levers hinged at an oblique angle to the vertebral column, and when acted upon by the intercostal muscles, the movable sternum to which they are attached ventrally, moves farther away from the relatively stationary backbone, thus enlarging the thoracic cavity in which the lungs are located. It thus comes about that inspiration is effected not only by the depression of the diaphragm but also by the elevation of the ribs, both efforts calling for muscular activity.

Expiration, on the other hand, is to a large extent automatic through the elasticity of the stretched body walls, the taut cartilaginous ends of the bent ribs, and tensity of expanded lung tissues.

In big, heavy animals, abdominal or diaphragmic breathing predominates over rib breathing. Jumping animals, like kangaroos and monkeys, utilize rib muscles rather more than the diaphragm for this purpose. Breathing by means of the ribs is also more pronounced in human females than in males, in which abdominal breathing predominates. The reason for this sexual difference in the respiratory mechanism, may be an evolutionary adaptation, brought about in connection with pregnancy, during which period the presence of a growing fetus interferes somewhat with freedom of movement of the diaphragm.

CHAPTER XIV

OUTGO APPARATUS (EXCRETORY SYSTEM)

I. EXCRETION

An inevitable consequence of the metabolic processes characterizing living creatures, is that various by-products are formed in the body which must be got rid of, since they are not only useless to the organism but may become decidedly harmful if retained. The mechanism for effecting this removal is the *excretory apparatus*, and, since there are many kinds of animals, there are several different devices for accomplishing the universal function of excretion.

The substances eliminated by excretion may be in the form of gases, solids, or liquids. Lungs and gills furnish the principal mechanism for the excretion of the inevitable gas, carbon dioxide, resulting from the respiratory oxidation of tissues, while the digestive tube is the avenue of escape for the solid refuse from ingested food. Although the latter may not be regarded as true excretion, since the solids evacuated have never been incorporated as a part of the body, it is nevertheless an indispensable part in the process of the disposal of waste. Both of these methods of elimination have already been considered in the chapters upon the digestive and the respiratory apparatus.

In addition to these two methods of disposal of the unusable products of the body there is also a constant excretion, or sloughing off, of cellular material from the epithelial surfaces of the body, both from the outer exposed surface, and also from the lining of various tubes and ducts which have access directly or indirectly to the outside.

The present chapter is concerned primarily with the urinary apparatus for the disposal of *liquid* waste, which is ordinarily referred to as the excretory system.

As a matter of fact liquid, or water in various guises, is excreted from the animal organism through several different channels. It is thrown off from the lungs and sweating skin of mam-

mals as vapor, from the digestive tract as the fluid component of the feces, and above all from the kidneys in the form of urine. It comes to the kidneys from the blood, charged with salts in solution, both organic and inorganic, together with a variety of other chemical substances, as well as cell wreckage of various sorts.

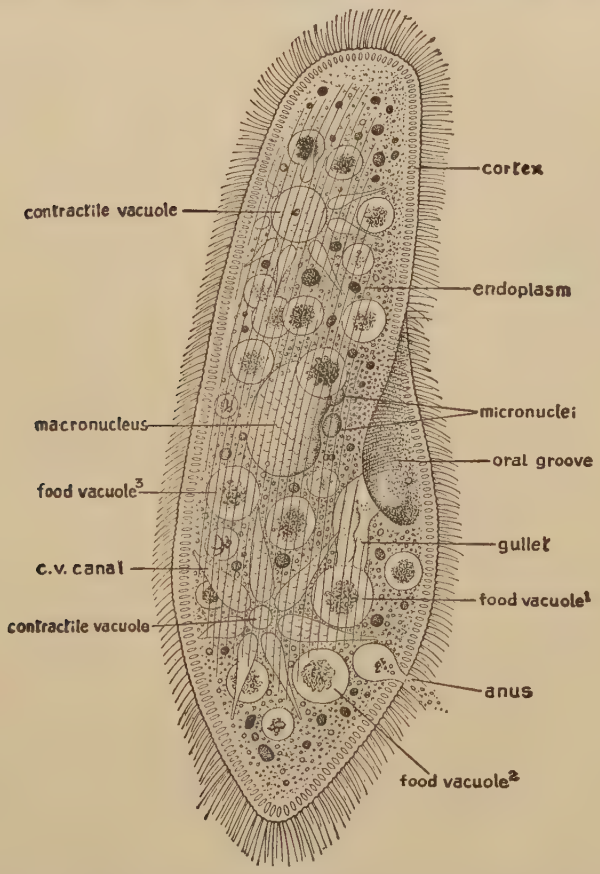


Fig. 349.—*Paramecium* viewed from the side. (From Hegner, after Pfurtscheller.)

Probably the simplest urinary apparatus of excretion is the *contractile vacuole* in Protozoa, which periodically expels to the outside its liquid contents, accumulated from the surrounding substance of the cell (Fig. 349). In higher animals, having a body cavity, drainage tubes, or *nephridia*, represent the

most primitive device for the elimination of liquid waste. When nephridia occur in invertebrates they are typically independent of each other, but in vertebrates they are more or less massed together into definite organs of excretion, called the *kidneys*. Generally they open at one end into the body cavity and at the other, through a common connecting duct, either directly or indirectly to the outside, thus furnishing a means of escape for the cœlomic fluids which receive contributions from all parts of the body. This arrangement is of particular significance in many invertebrates, such as worms for example, but decreases in importance in the vertebrates, where, with the lessening usefulness of the cœlomic fluid and the elaboration of a closed blood system, the liquid wastes are collected by the blood stream, rather than by finding temporary sanctuary in the cœlome.

The excretory system of the vertebrates may thus be described as fundamentally made up of nephridia, more or less completely emancipated from an original direct connection with the body cavity, but still in intimate contact with the blood stream, whence they transmit the waste materials to the outside through a duct of exit. The nephridial tubes of the kidneys have much in common with the sweat glands of the mammalian skin, in that both are tubes with walls of secreting cells in close juxtaposition to capillaries. When it is remembered that there are over two million sweat glands in an ordinary adult human being, and that end to end they constitute over twenty-five miles (Macfie) of secretory tubing, it will be realized that these "microscopic kidneys" are no insignificant understudies to the kidneys themselves in the disposal of waste materials from the body.

For purposes of general description the urinary apparatus of a typical vertebrate may be considered under three headings: (1) kidneys; (2) urinary ducts; and (3) bladders.

II. KIDNEYS

1. Form

In the shape of the paired kidneys the evolutionary tendency is towards compactness, consequently there is a certain parallel between their form and the general contour of the body. Thus the kidneys of the primitive eel-like cyclostomes are long strap-shaped bands, while in fishes generally they extend nearly throughout, if not the entire length of the body cavity. Frequently

too, the typical shape of the kidneys of fishes is modified to conform to the presence of the swim bladder, which in fishes is a bedfellow of these organs.

Among amphibians the wormlike Apoda and the long-bodied urodeles have correspondingly elongated kidneys, narrower anteriorly and widening posteriorly, while in the squat Anura they become much more compact and rounded in shape.

In lizards and alligators, which superficially resemble urodeles, the relation between the shape of the kidneys and the form of the body is less marked. The kidneys are still, however, somewhat elongated, and in turtles they become decidedly compact, conforming to the rigid requirements in space imposed by the shell. The opposite extreme is shown by the snakes where the kidneys are not only attenuated like the body but are also entirely crowded out of their typical side-by-side position, coming to lie tandem-fashion, one behind the other.

Fig. 350. — Left lobulated kidney of a bear, partly dissected. (After Henle.)

In birds the concavities of the elaborate pelvis, into which the kidneys are mostly packed, form a restricted bony casket that determines their lobulated form, but in spite of considerable variation in form, the highest degree of compactness is found among mammals. For example, mammals, such as the bear (Fig. 350), ox, seal, walrus, and porpoise, have lobed kidneys, a condition appearing also in human embryos but which becomes obliterated soon after birth.

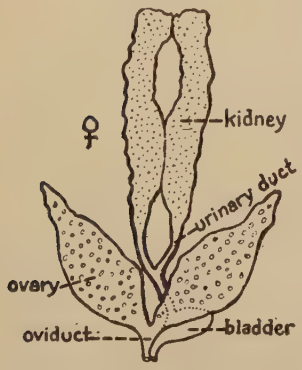


Fig. 351. — Semi-diagrammatic urogenital apparatus of teleost. (After Roule.)

Fusion of the two kidneys occurs frequently in teleost fishes (Fig. 351), and in many birds, and is not unusual, at least at the posterior end, in certain lizards. Exceptionally posterior fusion may occur even in man, when a so-called "horseshoe kidney" is formed.

If for any reason one of the two kidneys is put out of commission, the other usually enlarges and, as a "compensating kidney," takes over the function of its incapacitated mate.

2. Position

The kidneys are always closely associated with the dorsal wall of the body cavity, where they lie underneath the peritoneum. In fishes and birds they fit with intimate snugness, along either side of the backbone, but in amphibians, reptiles, and mammals they are less closely attached to the body wall and may project, or in mammals even hang free in the body cavity. Frequently the kidneys of fishes may extend even beyond the cœlome into the tail, while the blood supply of these organs, unlike that of higher vertebrates, is both arterial and venous, since it comes not only from the dorsal aorta but also from the tail, as the renal portal system.

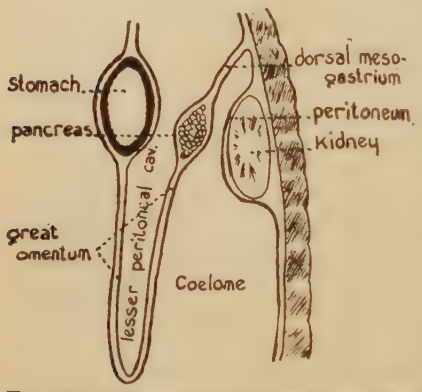


FIG. 352.—Diagram of the great omentum, showing position of the kidney behind the peritoneum. (After Huntington.)

In most reptiles the evolutionary trend of the kidneys to become compact as well as to migrate to a posterior position in the body cavity, is plainly shown. In birds, with the kidneys packed in the pelvis, the tendency to posterior migration has reached its limit. The kidneys of mammals lie rather freely in the body cavity, enclosed in a peritoneal envelope which is carried along before them during development as they push their way from behind the peritoneal wall in among the cœlomic viscera (Fig. 352).

Symmetry of position, which is definite in birds whose kidneys are rigidly arranged side by side in regular depressions of the pelvis, is less apparent in mammals where one kidney is usually not exactly opposite the other. In man the left kidney is ordinarily situated at a higher level than the right, although there are many exceptions to this arrangement.

3. Gross Structure of the Human Kidney

The human kidney is shaped like a "kidney" bean, and is surrounded by a connective tissue capsule, the *tunica fibrosa*.

It weighs about four and one-half ounces and, in its three major dimensions, usually measures slightly more than four by two by one inches. It has a convex outer, and a concave inner margin. The depression of the concave margin is the *hilus*, where the *renal artery* and *renal nerves* go in, and the *renal vein* and *ureter* make their exit.

When split lengthwise the kidney is seen to be a hollow organ with walls of very unequal thickness. The eccentric cavity within

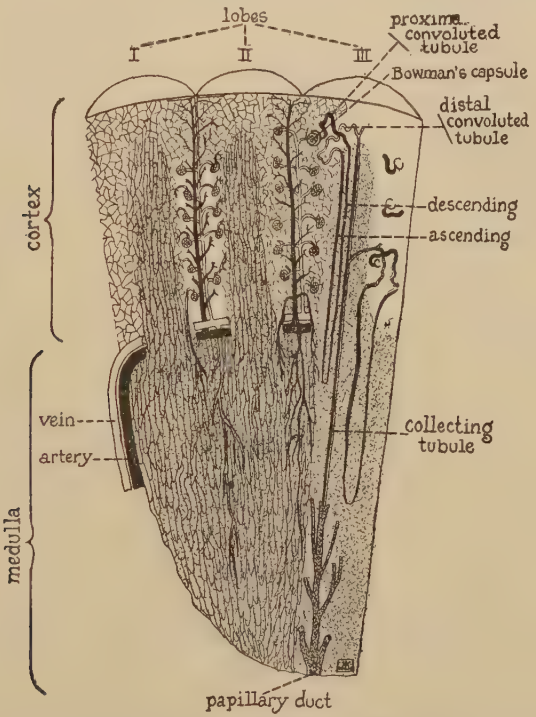


FIG. 353.—Diagram of three lobes of a kidney, showing the relation of a urinary unit to the circulatory system. (After Szymonowicz.)

the kidney is known as the *renal pelvis*. This is a funnel-shaped expansion of the urinary duct, or ureter, occupying the concave side of the kidney with the thin part of the wall next the hilus, and a thicker, more extensive wall surrounding the cavity around the convex side. This thicker wall is the solid substance of the kidney itself, and appears to the naked eye to be differentiated into a narrow, outer, rather uniform *cortical zone*, and a wider, inner, more diversified *medullary zone* (Fig. 353). The latter is made

up of from seven to twenty coneshaped segments, *Malpighian pyramids*, the bases of which rest against the cortical layer while the apices (*papillæ*) project into the cavity of the pelvis. Each cup-shaped diverticulum of the pelvis fits around a papilla and is called a *calyx*. The narrow outer layer of the cortex, upon which the bases of the Malpighian pyramids rest, lies just underneath the tunica fibrosa, and has a striated appearance, due to the presence of *cortical rays*. Extending inward from the zone of the cortical rays between the Malpighian pyramids, are the *columns of Bertini*, which are largely made up of the vascular subdivisions of the renal arteries and veins on their way to and from the Malpighian pyramids where they encounter the renal tubules of excretion.

The relation of all these microscopic structures will be clear after the microscopic structure of the *urinary units* composing the Malpighian pyramid, has been described.

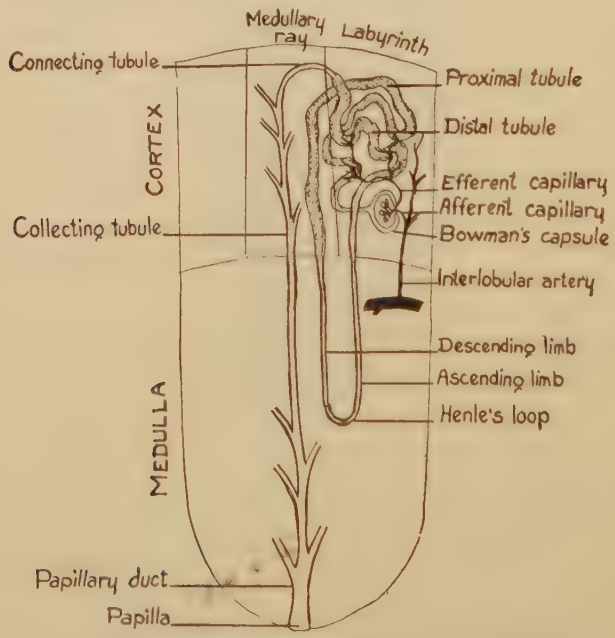


FIG. 354.—Diagram of a urinary unit. (After Piersol.)

4. A Urinary Unit

A urinary unit is a transformed nephridium that has gained an intimate contact with the blood system and established an avenue

of drainage to the outside. The various parts of such a unit are pictured in Fig. 354.

The junction where the nephridial tube reaches the blood system is called the *renal corpuscle* (Fig. 355). It consists of a spherical tuft of capillaries (*glomerulus*) enveloped by a double layer of epithelial cells (*Bowman's capsule*) between which is the cavity of the renal tubule.

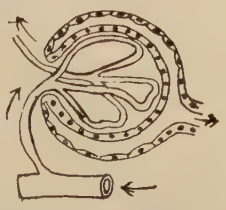


Fig. 355.—Renal corpuscle, consisting of a capillary loop (*glomerulus*), enclosed in a double cup of endothelial cells (Bowman's capsule).

The formation of Bowman's capsule around the glomerulus is brought about by the inpushing of the blind end of a nephridial tube by the glomerular knot of capillaries, much like pushing in the finger tip of an empty glove from the outside (Fig. 356). The delicate inner wall of Bowman's capsule is closely adherent to the glomerulus, so that the blood of the glomerulus is separated from the cavity of the nephridial tube only by two exceedingly thin layers, that is, the inner layer of Bowman's capsule and the wall of the glomerular capillary itself. Thus, the filtration of the liquids to be excreted from the blood into the nephridial tube, is greatly facilitated.

Once through the inner wall of Bowman's capsule, the excretory filtrate passes down through the *neck* into a thick-walled, kinked-up portion of the tube, the *proximal convoluted tubule*, whence it continues around a hairpin curve (*Henle's loop*) into a second thick-walled, kinked-up part, the *distal convoluted tubule*, which opens in turn into a *collecting tubule*. Eventually the collecting tubules of neighboring units join into larger common channels, *ducts of Bertini*, which finally open into the renal pelvis of the kidney at the tips of the papillæ. As many as ten to twenty-four ducts of Bertini may empty into the calyx of the pelvis from a single papilla of the human kidney. It is the pelvis, or the enlarged end of the *ureter*, which, together with the *bladder* and *urethra*, establishes a highway of communication with the outside world.

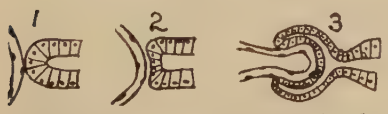


Fig. 356.—Successive stages in the formation of a Bowman's capsule. (After Bailey.)

Thus the entire urinary unit from the glomerulus to the opening

of the ducts of Bertini into the pelvis, is a continuous canal, the walls of which vary much in character and function. In the convoluted portions, which are in intimate contact with the capillary network of the glomerulus, the cells of the thickened wall have the power to extract substances from the blood, particularly waste organic nitrogenous compounds, such as urea and uric acid, that characterize urinary excretion.

According to Haidenhein's theory, the water of liquid excretion, with inorganic salts in solution, is largely derived by filtration from the glomerulus through Bowman's capsule, while nitrogenous organic waste products are added by secretion through the walls of the convoluted tubules, particularly the distal portion, after having been already elaborated in the blood stream during its passage through the liver.

The capillaries of the glomerulus are entirely arterial, forming a *rete mirabile*, rather than an arterio-venous transition. The afferent twig from the renal artery enters the glomerulus, while the efferent branch makes its exit near by on the same side, thus

Fig. 357. Evolution of pyramids in different kidneys. (After Nuhn.)

forming a projecting capillary knot that pushes in the blind end of the renal tubule to form Bowman's capsule. Upon leaving the renal corpuscle the efferent twig of the glomerulus soon breaks up into a capillary network which envelops the convoluted tubules, whence it emerges as a venous capillary, connecting eventually with the renal vein on its way out of the kidney.

It will now be seen that the Malpighian pyramids are masses of urinary units crowded together side by side, and that the columns of Bertini are the highways for the blood supply of these units. A minimum amount of connective tissue holds these parts together.

The kidneys of many mammals, for example, marsupials, insectivores, rodents, carnivores, perissodactyls, and apes, are *unipyramidal* with but a single papilla (Fig. 357). These kidneys

are never lobed, for the number of pyramids determines the number of lobes. The true multilobed condition of the human kidneys, which is most plainly apparent at about the fourth fetal month, is masked by the growth of parts which eventually fill in the superficial interstices between the lobes.

III. URINARY DUCTS

The ducts that drain the paired kidneys are usually two, although some fishes may have six or eight supplementary ducts when the nephridial organs extend into the massive tail region. In higher forms the urinary ducts are termed *ureters*. They are tubes with comparatively small bore and with muscular walls, so that the continuous product of the kidneys is forwarded on its way regardless of the position of the body, not by gravity alone but by peristalsis of the walls of the excretory ducts.

The length of the ureters depends upon the position of the kidneys within the body cavity. They are very long in snakes and extremely short in birds. In adult man they average from eleven to fourteen inches in length.

Urinary ducts terminate in a variety of ways. In bony fishes, male amphibians, and monotremes, they unite with the sexual ducts into a common channel, or *urogenital canal*, opening at the genital aperture. In elasmobranchs, most reptiles, and birds, they debouch into the cloaca, while in mammals they open into a reservoir, called the *bladder*, whence by a second duct, the *urethra*, the outside is finally gained.

IV. BLADDERS

The continuous excretion of liquids from the kidneys has given rise to the necessity for a temporary storage sac, the bladder, which may be emptied at suitable intervals. There are three general types of urinary bladders; tubal, cloacal, and allantoic.

Tubal bladders, which are present in most fishes from the ganoids on, are formed by the widening or enlargement of the urinary ducts. In many fishes two independent bladders may form (*vesica duplex*, Fig. 358, A), one near the end of each urinary duct, with the ducts afterwards uniting into a common passage-way of exit; or the two expansions may run together into a common

bilobed structure (*vesica bicornis* Fig. 358, B), as in *Lepisosteus* and some other ganoids; or, finally, the two excretory ducts may first join and then expand into a single bladder (*vesica simplex*) (Fig. 358, C), as, for example, in the pike, *Esox*. In all these cases the urinary ducts enter at one end of the bladder, while the exit is made at the opposite pole. The tubal bladder is most in evidence in teleost fishes, like the Pleuronectidæ, in which the swim bladder is absent, and it is frequently larger in the female than in the male. It is somewhat difficult to account for the presence in fishes of this structure, apparently useless and yet rarely absent.

The *cloacal bladder* occurs in Dipnoi, Amphibia (Fig. 359), and Monotremata. It is a diverticulum of the cloacal wall opposite

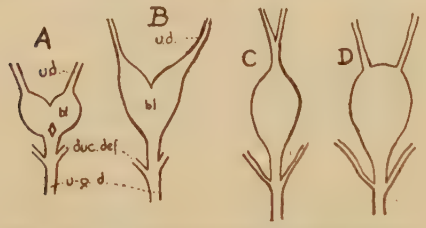


Fig. 358.—Various types of urinary bladders in fishes. *A*, duplex type in *Gadus; B*, bicornis type in *Lepisosteus; C and D*, simplex type with united urinary ducts. *bl*, bladder; *u.g.d.*, urogenital duct; *u.d.*, urinary duct; *duc. def.*, ductus deferens. (After Nuhn.)

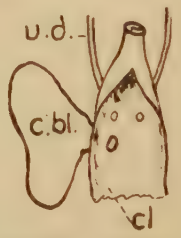


Fig. 359.—Cloacal bladder of an amphibian. *c.bl.*, cloacal bladder; *cl.*, cloaca; *u.d.*, urinary duct.

the point where the urinary ducts, with which it has no direct connection, enter. It is dorsal in the lungfishes and ventral in the amphibians. In the perennibranchiate amphibians it is considerably elongated, but rounded or broadened in the Anura. Frequently it is bilobed, as in frogs and toads, while in some urodeles, for example, *Salamandra*, *Triton*, and *Eurycea*, the lobes are prolonged into "horns." Cloacal bladders may become filled from the urinary ducts entering the cloaca, upon closure of the outer cloacal sphincter, and the backing up of the urinary secretion into the sac. They are of doubtful service and possibly belong in the category of preadaptive organs, with a future rather than a present utility.

The *allantoic bladder* according to most embryologists arises by the enlargement of the proximal, or basal, end of the embryonic

allantoic stalk (Fig. 360, D). Arey [1] says, however: "Contrary to earlier views, the allantois contributes nothing to the bladder or urachus." It is characteristic of mammals and such reptiles as turtles and some lizards that have a bladder. In the case of other amniotes, as snakes, crocodiles, many lizards, and birds, the whole allantois degenerates without developing a bladder. In mammals, according to one view, that part of the allantois left within the body wall when the umbilical cord connecting with the placenta is severed, enlarges to form the bladder.

As would be expected from its manner of origin, the embryonic bladder is elongated and fusiform in shape, the distal internal part of the umbilical cord becoming the *urachus*, or *vesico-umbilical ligament* (Fig. 360, D), anchoring the bladder to the inner wall at the umbilicus. Thus, one part of the allantoic stalk within the body wall enlarges into a hollow sac, while directly continuous with it the remainder of the stalk undergoes quite a different fate in becoming a ligament utilized as a guy rope. The occurrence of an occasional urachal cyst in man, with urine escaping by a fistula through the umbilicus, apparently demonstrates the embryonic derivation of the urachus and the bladder from a common allantoic origin. According to another view the mammalian bladder is a derivative of the embryonic cloaca.

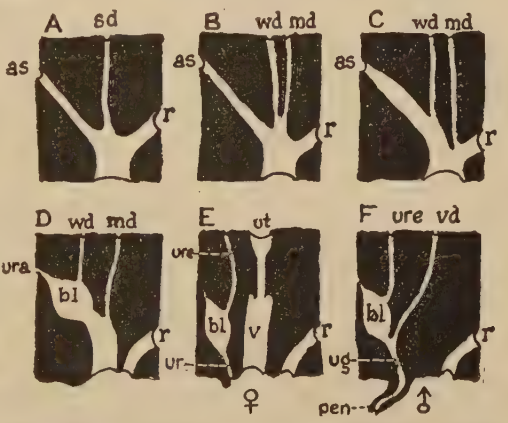


FIG. 360. — Evolution of the urogenital ducts. *A*, cyclostome stage; *B*, teleosts; *C*, male amphibians; *D*, female amphibians; *E*, female mammal; *F*, male mammal. *as*, allantoic stalk; *bl*, bladder; *md*, Müllerian duct; *pen*, penis; *r*, rectum; *sd*, segmental duct; *ug*, urogenital duct; *ur*, urethra; *ura*, urachus; *ure*, ureter; *ut*, uterus; *vd*, vas deferens; *wd*, Wolffian duct. (After Roule.)

The mammalian bladder is lined with mucous membrane and coated with peritoneum. It has a highly muscular wall, well supplied with nerves and blood vessels, the muscle fibers being largely

[1] *Developmental Anatomy*, pp. 147–8.

diverted from their originally regular longitudinal and circular arrangement, so that they interweave like felt in many directions. The result is that upon contraction the cavity of the bladder becomes smaller in all dimensions like a leaking toy balloon, rather than collapsing like a hot-water bag from which the water is emptied.

The exit from the bladder is from a single duct, the *urethra*, the entrance to which is kept closed by a muscular sphincter except upon periodic occasions when, upon the relaxation of the sphincter, the urine is expelled by the contraction of the muscular walls of the bladder.

Fig. 361.—Diagram of the diagonal passage of the ureter through the wall of the bladder. As the bladder becomes distended the pressure in the direction of the arrow tends to close the ureter.

There is considerable variation in the location where the ureters enter the bladder. Only rarely, as in *Lepus* and *Hyrax*, do they come in, as in fishes, at the opposite pole from the urethral exit. In most mammals they enter low down, near the urethra by an oblique passage through the wall of the bladder (Fig. 361). This arrangement makes the backflow of the urine into the ureters difficult, particularly when the bladder is full, because the pressure from distension tends to close the bore of the ureters.

Some lizards have a compound bladder made up of both cloacal and allantoic components.

V. URINE

The composition of the urine varies enormously in different animals, and at different times in the same animal. This is because the blood from which urinary secretion is obtained by the kidneys, is such a kaleidoscopic, modifiable fluid tissue, reflecting constantly different states of metabolism within the body. Furthermore, under pathological conditions still other variations from the normal in the composition of the urine appear. Consequently urine analysis is an important aid to the diagnostician in finding out what is going on within the body.

Carnivores generally have an acid urine, while that of herbivores tends to be alkaline, except when they are feeding largely upon milk. It is usually more concentrated in animals, such as turtles and birds, which drink sparingly.

Nitrogenous waste products, such as urea, creatinin, hippuric

acid, ammonia, and uric acid, characterize urine, although nitrogen-free organic constituents and inorganic substances, principally soluble chlorides of various sorts, are also present. In mammals, amphibians, and fishes, urea is the prominent nitrogenous compound present, while in reptiles and birds it is uric acid.

Mitchell[1] gives a table that accounts for about 99 per cent of the constituents in most normal human urines, in which 95.1 per cent is water; 2.55 per cent nitrogen-containing constituents; 1.26 per cent inorganic materials; and .052 per cent nitrogen-free substances.

VI. THE SUCCESSION OF KIDNEYS

1. In General

Although all kidneys are fundamentally nephridial tubes that extract liquid waste from the blood, the kidneys of different animals are by no means homologous structures.

Among the craniate vertebrates there are three kinds of nephridial structures serving as kidneys, that differ from each other not only in structure and position, in relation to the blood system and the excretory tubes, but also in their embryonic history. The three kinds of vertebrate "kidneys" are, as named by the English embryologist Balfour, the *pronephros*, of some cyclostomes; the *mesonephros*, of fishes and amphibians; and the *metanephros*, of reptiles, birds, and mammals.

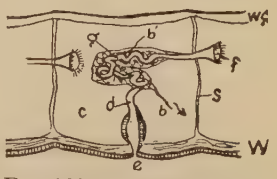


FIG. 362. — Diagram of a protonephridium of an annelid worm. *b.b*, blood vessels; *c*, cœlome; *d*, duct; *e*, external opening; *f*, nephrostome; *g*, glandular portion; *s*, septum; *w*, body wall; *wg*, wall of gut. (After Galloway.)

The higher vertebrates, whose kidneys are of the metanephric type, pass through preliminary pronephric and mesonephric stages before the permanent metanephric stage is reached. Thus, as is frequently the case, comparative anatomy and embryology have supplementary and confirmatory stories to tell about the same thing from different angles.

The nearest approach among invertebrates to the vertebrate nephridial apparatus is found in the *protonephridia* of annelid worms (Fig. 362), which, however, are not connected together by common excretory ducts to form excretory organs, as are the nephridia of all nephroi, but rather consist of several pairs of independent tubes, metamerically arranged.

[1] *General Physiology.*

2. The Nephridial Apparatus of Amphioxus

The nephridial apparatus of amphioxus is very much like that of the annelids. Instead of extending practically the entire length of the body with a pair in every segment, as in annelid worms, the protonephridia of amphioxus are localized in the anterior part of the body throughout the region of the gill slits. They lie somewhat above the pharynx near the dorsal region and may equal the gill slits in number. Each protonephridium is open and ciliated at its inner end, which communicates with the cœlomic sac, while at its outer end it empties independently into the peribranchial chamber surrounding the gills.

There are present no common excretory ducts for carrying away the excretion from the protonephridia, but the peribranchial chamber, with its atrial opening, accomplishes the same purpose while serving at the same time as the avenue of escape for the water of respiration.

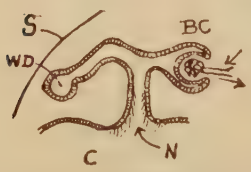


Fig. 363.—Diagram of the relation of the body cavity to a single nephridial element in vertebrates. *C*, cœlome; *N*, nephrostome; *WD*, Wolffian duct, leading to the outside; *BC*, Bowman's capsule; *S*, skin. When the nephrostome closes off, the body cavity no longer has direct drainage, but the excretion from the glomerulus in Bowman's capsule has direct access to the Wolffian duct. (After Brandt.)

Thus, the apparatus for urinary excretion in amphioxus is primarily concerned with cœlomic drainage rather than with direct extraction of urinary waste from the blood, and it consists not of a single pair of organs, or nephroi with their ducts, as in all true vertebrates, but of a series of independent paired excretory tubules, resembling those of annelid worms.

3. Pronephros

The pronephric tubules, *pronephridia*, are few in number and metamerically arranged along the anterior part of the body cavity. They originate as evaginations of the cœlomic epithelium along either side of the mesentery, and retain a ciliated mouth, or *nephrostome* (Fig. 363), opening into the cœlomic cavity. At the other extremity the pronephridia at first end blindly, but later join together down each side to form common *pronephridial*, or *segmental ducts*, opening to the outside (Fig. 364, A). Opposite and median to the nephrostomes of the prone-

phridia, a capillary ridge, the *glomus*, forms along the cœlomic wall (Fig. 365). This may be partly shut off from the general body cavity by a parallel fold of peritoneum. The sides of

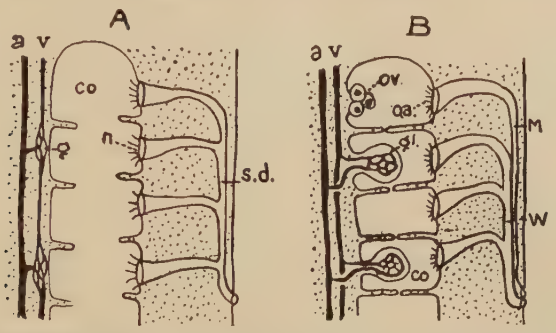


Fig. 364.—Diagram of the evolution of urogenital organs. *A*, pronephros stage; *B*, mesonephros stage; *a*, artery; *co*, cœlome; *g*, glomus; *gl*, glomerulus; *M*, Müllerian duct; *n*, nephrostome; *o.a*, *ostium abdominale*; *ov*, ovary; *s.d.*, segmental duct; *v*, vein; *W*, Wolffian duct. (After Haller.)

the pronephridial tubes come into close contact with the glomus along its course, (Fig. 365), so that there are two methods of obtaining excretion from the blood. It can pass by osmosis into the body cavity and be picked up by the current formed by the ciliated nephrostomes, or it can be extracted from the capillaries of the glomus by the secreting cells that compose the walls of the pronephridia, much in the same way that the secreting cells of the convoluted tubules obtain material from the blood of the capillary network in the case of the urinary unit. In either instance the liquid excreta are passed on through the pronephridia to the segmental duct, which disposes of the waste to the outside world. No encapsuling connective tissue surrounds the pronephridia, like the tunica fibrosa of the mammalian kidney.

Fig. 365. — Reconstruction of the pronephros of *Salamandra*. *a*, aorta; *c*, cœlome; *d*, pronephric duct; *g*, glomus; *1*, *2*, *3*, pronephridia. (From Kingsley, after Semon.)

The pronephroi are best developed in the cyclostomes, where they persist throughout life (Fig. 366), although replaced functionally in most cases by mesonephroi. It is probable that in some myxinoids, as *Polistotrema* or *Bdellostoma*, they remain the lifelong functional kidneys. They also persist structurally in some few teleosts. In

other vertebrates, particularly types like elasmobranchs and amphibians that have a larval development, they make a temporary embryonic appearance. In the shark, *Pristiurus*, there are four pairs of pronephric tubules, in the elasmobranch *Torpedo*, six, while in the legless amphibian *Cæcilia*, ten pairs of pronephridia hold the stage for a time during early development. Transient traces of pronephridia in mammals have been described, one or more pairs even having been identified in early human embryos.

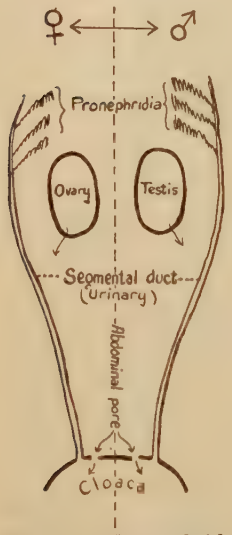


FIG. 366.—Pronephridial stage of certain cyclostomes. Female represented on the left; male on the right.

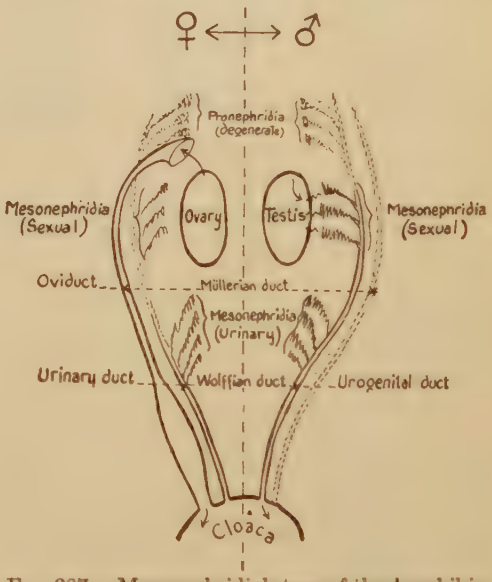


FIG. 367.—Mesonephridial stage of the Amphibia. Female represented on the left; male on the right.

Although the downfall of the pronephridia seems to be universal, with the possible exception in certain myxinoids already mentioned, the segmental ducts are more persistent and, as will be seen later, are retained to play an important part in the succeeding dynasty of the mesonephros.

4. Mesonephros

The second type of kidney in the vertebrate succession is the *mesonephros* (Fig. 367). Like other kidneys, this structure

is made up of nephridial tubules, *mesonephridia* (Fig. 364, B), which in this case develop in the embryo in the dorsal and lumbar regions of the cœlome posterior to the pronephros though at a later time.

Mesonephridia, which are much more numerous than pronephridia, do not generally show the primitive metameric arrangement, although in the case of the hagfish, *Myxine*, this is retained throughout life. The most anterior mesonephridia are the oldest, and subsequent additions arise in the posterior direction. They originate independently and connect secondarily with the paired segmental ducts that hold over from the former régime (Fig 368).

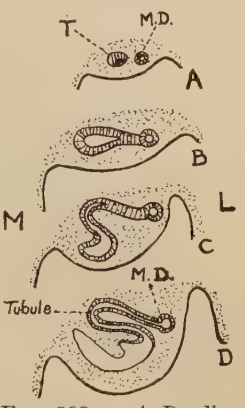


FIG. 368. — *A–D*, diagrams showing the differentiation of a mesonephric tubule. *L*, lateral; *M*, median; *T*, *anlage* of mesonephric tubule; *M.D.*, mesonephric duct. (From Arey, after Felix-Prentiss.)

Each mesonephros primarily forks at its inner end. One branch terminates with a nephrostome opening into the cœlome, while the other ends with a renal corpuscle by forming a Bowman's capsule around a glomerulus from the blood system (Fig. 369, B). The nephrostomes of some of the more anterior mesonephridia remain permanently open, particularly in the elasmobranchs and ganoids, while in the cyclostomes

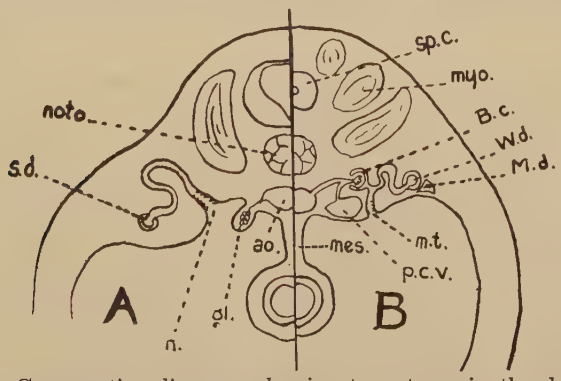


FIG. 369.—Cross section diagrams showing two stages in the development of the nephridia. *A*, pronephric stage; *B*, mesonephric stage; *ao*, aorta; *B.c.*, Bowman's capsule; *gl.*, glomus; *mes.*, mesentery; *m.t.*, mesonephric tubule; *M.d.*, Müllerian duct; *myo.*, myotome; *noto.*, notochord; *p.c.v.*, posterior cardinal vein; *s.d.*, segmental duct; *sp.c.*, spinal cord; *n*, nephrostome; *W.d.*, Wolffian duct. (After Wiedersheim.)

they are retained throughout the entire length of the organ, although they are for the most part obliterated. When the nephrostomes all become closed, as in amphibians and amniotes generally (Fig. 370, right side), the body cavity virtually becomes a closed sinus, and the peritoneal fluid with whatever excretion may be present in it, can only escape like other lymphatic fluids through the blood channels.

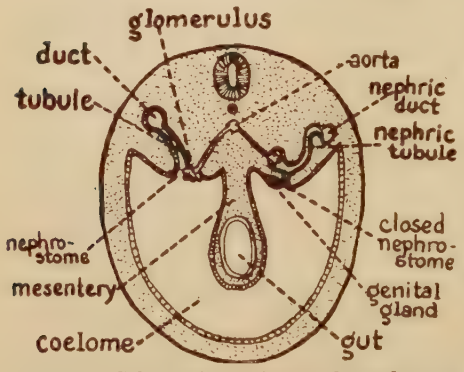


FIG. 370.—Schematic section to show the specialization of the dorsal part of the cœlome into nephric tubules and glomeruli. On one side the tubule and glomerulus remain in continuity with the cœlome; on the other side they are buried in the Wolffian ridge. (After Keith.)

The mesonephros functions throughout life in cyclostomes, with the exception of the hagfishes already mentioned as well as in fishes and amphibians. It also serves temporarily as the kidney for practically all other vertebrates until it is superseded in turn by the metanephros. In reptiles, as well as in *Echidna* and *Didelphys* among mammals, the mesonephros endures until sometime after birth, and, in the case of the lizard, *Lacerta*, even until after the first hibernation.

In most mammals the functional mesonephros is confined to the embryonic period, although occasionally, as in the guinea pig and mouse, it degenerates so early that it probably never functions as a kidney at all. In man the mesonephros, or *Wolffian body*, reaches its highwater mark during the second month of fetal life when it appears as a slightly projecting ridge on either side along the dorsal part of the cœlome from the posterior cervical region to the pelvis, where the two ridges fuse into one.

The drainage ducts of the mesonephroi are the persisting segmental ducts of the pronephroi, which in their new rôle are termed *Wolffian ducts* (Fig. 367). Thus, if the whole mesonephros is compared to a "gland," which it certainly resembles, whose secretion is delivered through a duct, there is one striking difference to be noted between it and an ordinary gland, namely, the

duct is formed before the secreting part is developed, and independently of it.

When the mesonephros degenerates and gives way to the metanephros in reptiles, birds, and mammals, many of its component parts are salvaged and utilized for other purposes in connection with the reproductive system.

The whole mesonephros, at least in its cœlomic aspect, is cased in a peritoneal envelope, and is a much more compact and unified organ than its pronephric predecessor.

5. Metanephros

The third and last type of vertebrate kidney, which replaces the mesonephros in reptiles, birds, and mammals, is the *metanephros*. Its nephridial tubules, the *metanephridia*, which have been already described as "urinary units," take their origin in the tissue surrounding the posterior part of the Wolffian ducts in the sacral region of the body, ventral to the sacrum and dorsal to the cloaca when this is present (Fig. 371).

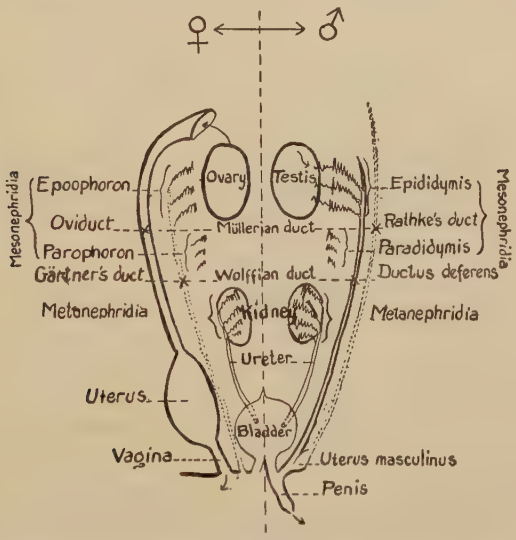


FIG. 371.—Metanephridial stage. Female represented on the left; male on the right.

The metanephridia are very numerous, elongated, and highly modified histologically. They are massed together inside of a tunica fibrosa, so that, particularly in the mammals, they form

kidneys more independent of the cœlomic wall than either pronephroi or mesonephroi. In position the metanephridia are posterior to the last mesonephridia and they develop at a later time, although beginnings of a metanephridial system put in an appearance at the posterior end of the mesonephros in some teleost fishes. A nephrostome is never present and consequently at no stage do the metanephridia communicate with the cœlome. As a result of the absence of that branch of the nephridial tube bearing the nephrostome, the connection with the blood system, that is, the Malpighian corpuscle, appears to be at the blind end of the tubule and not on a side branch as in the mesonephridium.

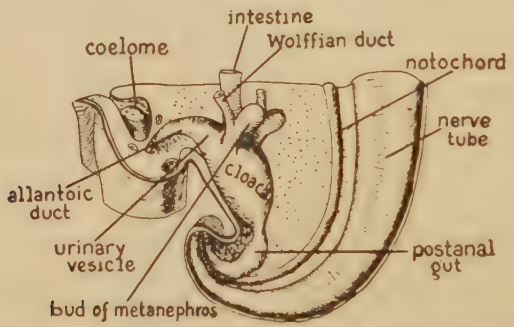


Fig. 372.—The cloaca of a human embryo of about 26 days, showing beginnings of ureter. (From Keibel's model.)

An entirely new pair of excretory ducts, the true *ureters*, sprout out from the base of the Wolffian ducts (Fig. 372), and with these the metanephridia eventually connect. Meanwhile the Wolffian ducts, shorn of their former excretory function, are turned over to the service of the reproductive system, as sperm ducts in the male, while in the female they degenerate.

In man the metanephros, or permanent kidney, assumes dominance during the third month of fetal life, and the remains of the mesonephros become accessory to the reproductive apparatus, as will appear in the next chapter.

CHAPTER XV

PRESERVATION OF SPECIES (REPRODUCTIVE SYSTEM)

I. THE SIGNIFICANCE OF REPRODUCTION

The individual is the triumphant outcome of the age-long interaction of all the mighty and intricate forces of evolution. The various mechanisms of metabolism thus far considered, including the integumentary, digestive, circulatory, respiratory, and excretory systems, as well as the mechanisms of motion and sensation which are to be described in Part III, all contribute directly to the development of the individual. There is, indeed, only one other concern in nature of greater moment than the upkeep and well-being of the individual, and that is the establishment of a continuation on the face of the earth of these precious products of evolutionary travail, which have "won a place in the sun." However, there was never a single individual, even among mankind, of such supreme importance that it could not be spared. This is fortunate, for it is the fate of every organism eventually, like any other delicate piece of machinery, to break down or wear out.

Filling the gaps caused by death in the rank and file of organic life may be regarded as a matter of *extra growth beyond individual requirements*. The surplus thus gained may become detached from the original organism to form a new and independent individual. Detachable excess growth material, endowed in this way with the capacity to reconstruct a new individual, is termed *germplasm*. It forms the *continuum* which joins generations together so that any particular organism represents the ultimate link in an unbroken chain of organisms extending back into the past farther than the imagination can go. In this way the torch of life is not extinguished but is handed on.

To insure the life of the species by replacement is the part of *reproduction*. This is an altruistic function, quite different from the selfish function of individual maintenance, and frequently its exercise is accomplished at the expense, or even the sacrifice, of individual life.

II. THE ESSENTIAL REPRODUCTIVE CELLS

In describing the mechanism of sexual reproduction it is important to distinguish clearly the essentially "immortal germplasm" (Weismann) that bridges the generations, that is, the sperm and ova, from the accessory bodily structures which minister thereto, but which are destined to perish with the individual of which they form a part. *Germplasm is the essential material concerned in reproduction.*

1. Sperm

The detachable germinal units derived from the male individual, are *sperm cells.* They are frequently called "spermatozoa," (*sperma,* seed; *zoön,* animal), an awkward, misleading word, which embalms the historical fact that when these cells were first discovered by the early microscopists, they were thought to be tiny parasitic animals (Fig 373).

Fig. 373.—Spermatozoan ("animalculum") of a man, according to Leeuwenhoek, 1678. (After Hesse.)

A sperm cell, in order to produce a new individual, must always join forces with an egg cell, whereas such a union is not indispensable in the case of the egg cell which, among certain invertebrates, may develop parthenogenetically, that is, without the assistance of a male cell.

Sperm cells have a chemical specificity for the eggs of their own kind so that the different species of animals, even though they may have free access to each other, as in sea water for example, do not bastardize under ordinary conditions.

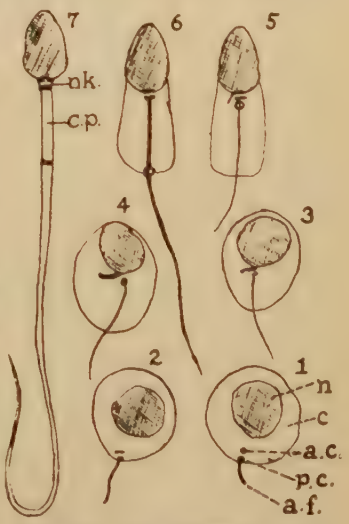


Fig. 374.—1–7, stages in the development of sperm cells. *a.c.*, anterior centrosome; *a.f.*, axial filament; *c*, cytoplasm; *c.p.*, connecting piece; *n*, nucleus; *nk.*, neck; *p.c.*, posterior centrosome. (After Meves.)

The motility which enables the active sperm to seek out the comparatively stationary eggs, is accomplished among vertebrates

by a vibratile "tail," which sculls the cell body forward through a liquid medium. Certain invertebrates, however, such as some of the nematode worms, arachnids, mites, myriapods, and many crabs, have ameboid sperm cells which creep to their destination in contact with a substrate instead of swimming freely through an intervening fluid.

The details of structure of a typical sperm, together with an indication of the way in which a spermatozoön reaches its highly specialized form from a generalized embryonic shape, are shown in Fig 374.

The number of sperm cells produced by male animals of different species is greatly in excess of the number of eggs furnished by

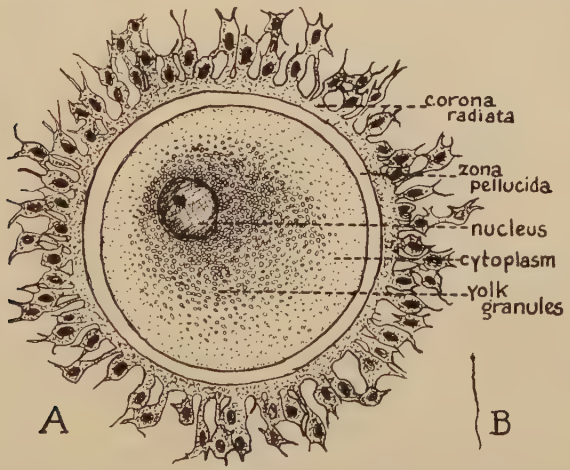


Fig 375.—*A*, human ovum, approaching maturity, examined fresh in *liquor folliculi*, much enlarged. The *zona pellucida* appears as a clear girdle, surrounded by the cells of the *corona radiata*. Yolk granules in the cytoplasm enclose the nucleus and nucleolus. *B*, a human sperm, correspondingly enlarged. (After Waldeyer.)

corresponding females. It has been estimated by Professor Shipley that in man, for instance, the total number of sperm cells produced throughout the duration of sexual life, may be 340 billion, while the eggs that come to maturity during the lifetime of a female will hardly exceed 400. This makes the ratio of possible sperms to eggs in the human race something like 850,000,000 to 1.

There is a corresponding discrepancy in *size* between the male and female germ cells (Fig. 375), yet it is a demonstrated fact that

the egg and sperm are essentially equal partners with respect to the hereditary chromosomal determiners which each sex contributes to the mutual enterprise of a new individual.

The viability of sperm cells after detachment from the male, likewise shows great variation. Haempel gives the duration of the independent life in water of the sperm of certain fishes, as follows:

Trutta fario, L.	23 seconds
Trutta viridea, W. Gibb.	40 "
Trutta salar, L.	45 "
Salmo hucho, L.	45 "
Barbus fluviatilis, Ag.	120 "
Esox lucius, L.	3–4 minutes
Cyprinus carpio, L.	5 "

According to Lewis, human sperm may retain activity for three days after the death of the individual, and if in the female genital tract, for a week or more. The sperm of bats remain alive and efficient from the time of pairing in autumn until the following spring, when the eggs are ready for fertilization.

2. Eggs

The *ova*, or germplasmal cells of the female, are less independent of the individual which produces them, than the sperm cells of the male. In many instances they tarry within the protective body for a considerable time after attaining potential independence, and may even undergo extensive development into a new organism, as, for instance, in mammals, before forsaking the maternal body of their origin.

The fact that the egg is fertilized by the sperm and not *vice versa*, has entailed the necessity of various additions to the egg cell itself, in the form of stored nutrition and protective envelopes for the forthcoming individual, which are entirely unnecessary in sperm cells.

The chief emergency ration stored in the egg is *yolk*. The quantity of such food in different species of animals, varies all the way from a chance fat droplet in certain protoplasmic eggs, to the relatively enormous supply which makes up the familiar yellow sphere of a hen's egg. In addition to yolk, the eggs of turtles, crocodiles, and birds, as well as of that most primitive living New Zealand reptile, *Sphenodon*, have a supply of albumen, or "white," wrapped around the yolk.

The eggs of amphibians are covered also with a glairy, albuminous coating, which has the property of swelling up into a thick, protective, jelly-like envelope, upon exposure to water (Fig. 376). This is why the mass of eggs which a frog or toad lays in water acquires, directly after deposition, a total size considerably larger than the entire body from whence it came.

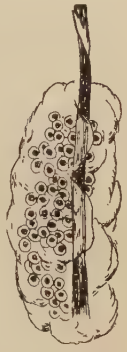


Fig. 376.—A bunch of frog's eggs attached to a stick. (After G. H. Herrick.)

Eggs that are not extruded into water, or which do not undergo development into embryos within the sheltering body of the female, are provided with some sort of a protective *shell*. This may be leathery, or of a texture like parchment, as in many reptiles, but it is usually calcified, being perforated by innumerable tiny air holes through which respiration can occur. The calcareous-shelled egg of the warm-blooded bird differs from that of the cold-blooded reptile, by the presence of a heavier, firmer shell, an air chamber at one end within the shell (Fig. 377), and a greater amount of supplementary albumen, a part of which develops into the *chalaza*, that anchors the egg at either end like a twisted guy rope, preventing undue mechanical disturbance. The chalaza also allows the yolk, bearing its precious protoplasmic germinal disc, to rotate within the shell so that the disc is always on top,

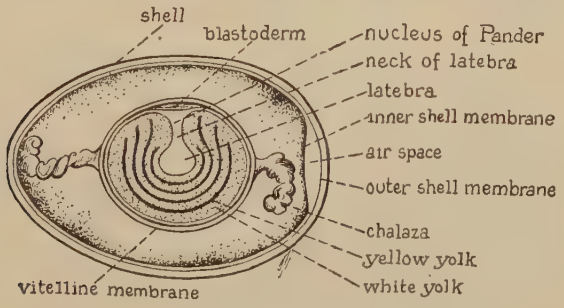


Fig. 377.—Egg of a bird. (After Schimkewitsch.)

regardless of the position of the egg as a whole. All of these additional modifications of the female avian germ cell are devices called forth by the necessity of egg laying and subsequent incubation.

In *shape* the eggs of vertebrates are typically spherical, particularly those of fishes and amphibians that are deposited in water, and those of mammals which do not require a shell because they are not exposed. The eggs of reptiles are usually elongated and elliptical, while those of birds are prevailingly oval, with one end more pointed than the other so that they pack economically within the confines of a nest. Most sea birds build shallow nests, depositing their eggs either in perilous crevices or in flat exposed situations, consequently their eggs taper so much that they do not roll away when disturbed, but simply pivot about in a circle, thus remaining safely in one place.

As already pointed out, the egg by reason of the presence of yolk and albumen, exceeds the sperm many times in size. The human egg (Fig. 375), is very small, but although only about 1/125 of an inch in diameter, it is nevertheless 50,000 times larger than a single sperm, which measures scarcely five micra in diameter.

FIG. 378.—Egg case of dogfish, *Scyllium*, cut open to show the embryo surrounding the yolk within. The egg case is prolonged into entangling tendrils. (From Schimkewitsch, after Home.)

The eggs of marine fishes are usually smaller and more numerous than those of fresh-water fishes, although elasmobranchs form a notable exception, as they have the largest eggs not only of any fishes but perhaps of any animal. H. Braus reports a specimen of the shark, *Hexanchus griseus*, that measured 4.2 meters in length and weighed 400 kilograms, from which he took out of a single ovary fifty-three eggs of approximately the same size, each measuring nine by eleven centimeters and weighing about 500 grams each. The eggs of certain Japanese characid sharks are known to attain the size of fourteen by twenty-two centimeters, which considerably exceeds the average of twelve by fifteen centimeters common to ostrich eggs.

The number of eggs produced bears a direct relation to the chances for attaining maturity. The elasmobranch fishes, the young of which are born alive and well advanced towards the stage when they can fend for themselves, produce only a few eggs

(Fig. 378). Prevost, for instance gives four to fourteen ova as the seasonal output of the elasmobranch, *Torpedo marmorata.* The stickleback, *Gasterosteus,* which makes a nest that is guarded by the male from devouring enemies, lays less than a hundred eggs. On the other hand the codfish, *Gadus,* whose unprotected eggs are exposed to the countless perils of the open ocean, broadcasts several million eggs during a single breeding season.

As one ascends the vertebrate scale from fishes through amphibians (Fig. 31), reptiles, and birds to mammals, there is seen to be an increasing provision for parental care, with a corresponding falling off in the number of eggs produced that suggests the mathematical computations and conclusions of an expert life-insurance actuary.

Large eggs require more yolk than small ones, and so there is a physiological, as well as a teleological reason for the correlation of numbers and size in egg production.

III. SECONDARY REPRODUCTIVE APPARATUS

As already indicated, eggs and sperm are the essential reproductive cells. They preserve and carry forward the traditions of each species, but in doing this they require a place of abode, devices for bringing the sex cells together in effective union, and provision for the safe development of the fertilized egg into a new individual. These aids to the germplasm are a part of the *somatoplasm* (Weismann), or the non-germplasmal body of the individual. From the viewpoint of the species, the body, or somatoplasm of the individual, may be regarded simply as a mortal vehicle for temporarily maintaining and transmitting the immortal germplasm.

The parts of the body that are in the direct service of the germ cells are (1) gonads, or organs that house the eggs and sperm; (2) ducts, that transmit the germ cells; (3) apparatus of various sorts for facilitating the union of the sex cells; (4) accessory glands; (5) devices for the care of the eggs before and after fertilization; (6) certain rudimentary organs of doubtful utility; and (7) modifications of the body that differentiate male from female, and which may possibly influence sexual behavior.

1. Gonads

The *gonads* are paired masses of mesodermal tissue that develop in the antero-dorsal part of the body cavity on either side

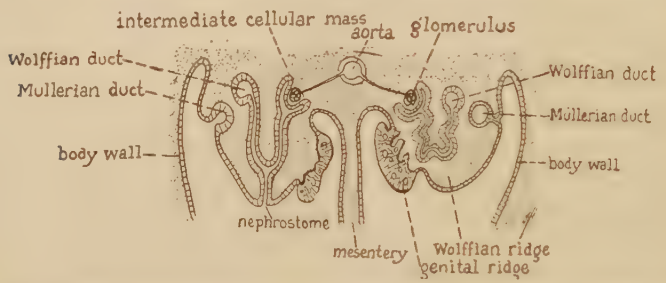


FIG. 379.—Diagrammatic cross section across the Wolffian and genital ridges, to show the origin and relations of the Müllerian ducts and tubules of the Wolffian body. (From Keith, after Pasteau.)

of the mesentery (Fig. 379). They become invaded by potential germ cells which like all other cells are the direct descendants by mitosis of the original fertilized egg, or the germinal material from which the animal arose (Fig. 380).

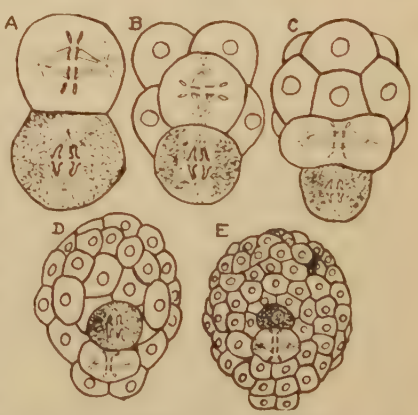


FIG. 380.—Separation of somatic and germplasmal cells in five stages in the developing embryo of the nematode worm, *Ascaris*. The darkened cells represent the germplasm, becoming, in *E*, the ancestral cells from which the eggs or sperm arise. All other cells by repeated division become the body of the worm. (After Meisenheimer.)

Gonads that harbor future sperm cells are called *testes*, and those that produce egg cells, *ovaries*. Among vertebrates, with a few exceptions to be mentioned later, the testes and ovaries develop in different individuals, that is, the sexes are distinct from each other.

In amphioxus there may be as many as twenty-six pairs of gonads (Fig. 13), that are superficially alike in both sexes and arranged metamerically along the gill region. The largest pairs are in the middle with the others decreasing in size at either end. In most vertebrates, however, there is not

more than a single pair of gonads, and consequently metamerism or segmentation disappears. In a few vertebrates only a single gonad is present, either as the result of fusion, as in the lamprey eel, or of unilateral degeneration, as in the hagfish and the single ovary of birds, while frequently one of a pair of gonads will be smaller than its mate.

The germ cells, which are the distinctive feature of gonads, arise from the embryonic entoderm, which never shows metameric arrangement in its development.

The shape of gonads is in general influenced by the form of the body of the animal to which they belong. Thus, in the worm-like amphibian, *Epicrinum*, they resemble a segmented chain; in urodeles they are long and spindle-shaped; and in frogs and toads, oval. Among reptiles it is easy to distinguish the gonads of the short, wide turtles, from those of elongated snakes, by shape alone.

During the breeding season gonads, particularly those of the prolific fishes, increase enormously in size with the multiplication and growth of the germ cells.

The gonads of males, that is, *testes*, are always more compact organs than the ovaries of corresponding females, a characteristic due in part to the difference in size of the germ cells that they produce.

A. Testes

The male gonads, which not only produce sperm cells but also an internal secretion, are double glandular organs, both *cytogenic*, or cell-producing, and *endocrinic*, or secretory without an outlet of ducts.

A single testis arises as a genital ridge along the ventro-medial border of the mesonephros, or *Wolffian body* (Fig. 379). In most of the lower vertebrates it maintains an intimate relation with the anterior part of the mesonephros, which in this region loses its excretory function, becoming transformed into a useful accessory reproductive organ, the *epididymis*, through which the sperm pass on their way to the sperm duct. Even higher up among the mammals the epididymal portion of the transitory mesonephros is still preserved as an integral part of the reproductive apparatus in the male, although the entire structure becomes rudimentary in the female, being represented only by

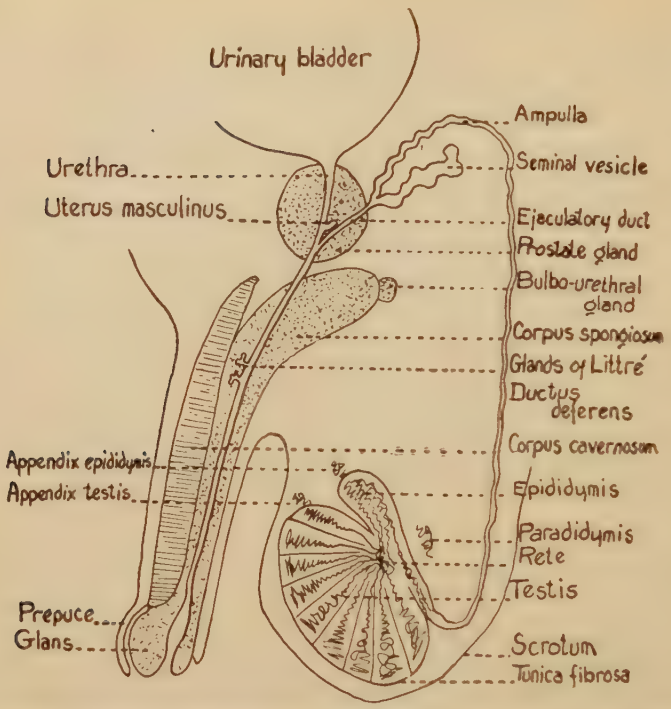


FIG. 381.—Diagram of the male genitalia in man. (From Jordan and Ferguson, after Merkel.)

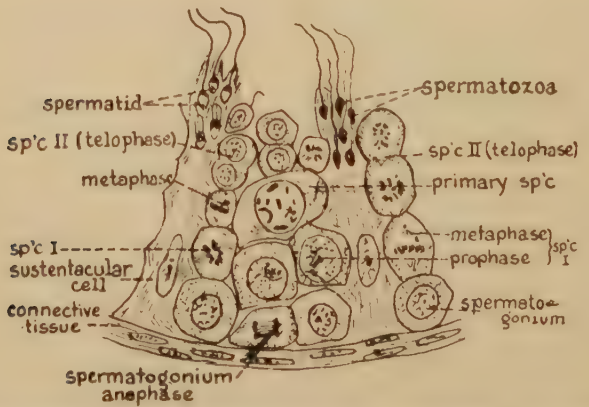


FIG. 382.—Stages in the spermatogenesis of man, arranged in a composite to represent a portion of a seminiferous tubule (X900) that has been sectioned transversely. *sp.c*, sperm cell. (After Arey.)

useless fragmentary remains that are frequently the foci for cystic formations and other pathological troubles.

The teleost fishes form a notable exception with respect to intimate dependence of the reproductive apparatus upon its nephridial neighbors, for in them the testis is entirely emancipated from the mesonephros, with no attendant epididymis.

The compact testes of mammals are oval bodies, enclosed in a close-fitting capsular sheath of connective tissue, the *tunica albuginea*, outside of which, on the free exposed surface at least, is a layer of endothelium, the *tunica vaginalis*, homologous with the peritoneum which lines the body cavity. Underneath the tough tunica albuginea is another layer of looser texture well supplied with blood vessels, the *tunica vasculosa*. Partitions of connective tissue extend from the tunica albuginea from one side to the other, dividing the testis into wedge-shaped compartments (Fig. 381), within which are lodged the *seminiferous tubules* that produce the sperm cells (Fig. 382).

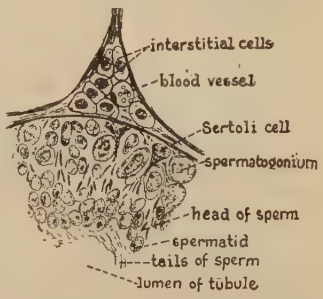


FIG. 383.—Parts of transverse section of three seminiferous tubules from the testis of a white mouse. (After Szymonowicz.)

Two sorts of cells are to be found within the walls of these tubules; first, the supporting, and possibly nutritive *Sertoli cells*, and second, the primordial germ cells, or *spermatogonia*, destined after repeated mitoses to give rise to the sperm. Between the tubules themselves are blood vessels and still another kind of cells, namely, *interstitial cells*, that form the endocrinal part of the structure (Fig. 383).

In man the seminiferous tubules (Fig. 384), of which there may be several hundred, are very much kinked-up for the most part of their length, (*tubuli contorti*), but they straighten out, (*tubuli recti*), as they focus together at the inner side of the testis. A single contorted tubule, occupying ordinarily a span of not more than an inch, stretches out when uncoiled to over a foot in length.

Tubuli contorti pass over continuously at their inner ends into tubuli recti, anastomosing together into a network of tiny passages, forming the *rete testis*, from which emerge other tubules, *ductuli efferentes*, that pass through the epididymis and

eventually reach the sperm duct, or *ductus deferens,* leading to the outside.

Both blood vessels and nerves reach the testis between two layers of endothelial tissue continuous with the peritoneum, thus forming the *mesorchium,* which serves as an anchoring bridge between body wall and testis in the same way that the mesentery serves the intestine.

FIG. 384.—Tubes of testis. *1,* tubuli contorti; *2,* rete testis; *3,* ductuli efferentes; *4, 6,* ductus epididymis; *5, 9,* ductuli aberrantes; *7, 8,* ductus deferens; *10,* paradidymis. (After Szymonowicz.)

The original anterior embryonic position of the testes within the body cavity, is by no means always maintained. There is an evolutionary tendency, particularly among mammals, for the testes to migrate backward during the course of development, and in the higher animals this tendency is carried to such an extreme that the testes forsake the body cavity entirely and come to hang outside in a sac of outpushed skin and muscle, known as the *scrotum* (Fig. 385). According to the degree of migration which the testes have undergone, animals in general may be separated into three groups, as follows: first, those in which the testes remain within the confines of the cœlome; second, those in which there is a temporary descent during periods of sexual activity, followed by withdrawal into the body cavity; and third, those with a permanent descent into the scrotum.

To the first group belong all vertebrates below the mammals, and, among mammals, monotremes, many insectivores, coneys, whales, and elephants. In the second group are many rodents, some insectivores, civet cats and otters among carnivores, llamas and camels, and some apes. Those with a permanent descent of the testes after the fetal period, include marsupials, most carnivores, most ungulates, and most primates.

The testes lie within a cavity in the scrotum which is homologous with the body cavity of which it was originally a part. As a result of this peculiar development there is a double layer of enwrapping peritoneum about the testis, one, the *parietal layer* lining the scrotal cavity itself, and the other, the *visceral*

layer, or tunica vaginalis already mentioned, that is reflected over the surface of the testis in close contact with the tunica albuginea.

The *inguinal canal*, that is, the continuous passage-way between the cœlome and the cavity of the scrotal sac, remains open in those mammals subject to a temporary descent of the testes, and it is also always pervious in marsupials, although in other mammals having a permanent descent, it becomes closed.

The wall of the scrotum is essentially the same as that of the neighboring body wall except that the skin is more highly pigmented and has a looser subcutaneous layer, and a greater supply of smooth muscle cells than the skin of other parts of the body.

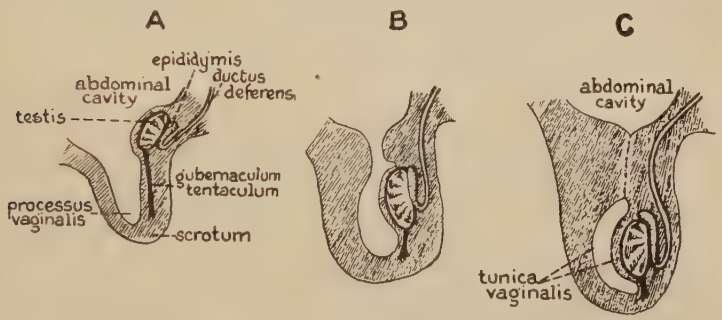


Fig. 385.—Three stages in the descent of the testes. (After Arey.)

In man the descent of the testes ordinarily occurs shortly before birth. When, however, the testes are abnormally retained within the cœlome, resulting in so-called *cryptorchism*, (*cryptos*, hidden; *orchis*, testis) this unusual state of affairs has a perfect explanation in the light of comparative anatomy.

In the tapir and rhinoceros there is no pendulous scrotum, but the testes leave the body cavity and lie in pockets close under the skin.

A similar anomalous condition is seen in some flatfishes (Pleuronectidæ), in which not only the testes but also the ovaries are crowded out of the cramped quarters of the body cavity and come to lie in pockets "extending backward into a kind of concealed scrotum between the integument and muscles on each side above the anal fin" (Owen).

Why the testes of the highest vertebrates, with their precious contents, should push out the body wall into a scrotal sac and

come to hang over the edge of the pelvic bones in so exposed a situation, is not apparent. Certainly the outpushing of the body wall by the protruding testes leaves centers of structural weakness that entail liability to hernia and frequent attendant troubles.

Recent work by Moore[1] seems to indicate that temperature as high as that normally maintained within the mammalian body, is somewhat detrimental to the development of spermatozoa. The descent into the scrotal sac is a device whereby the testes are subjected to a lower temperature than that within the body cavity, thus favoring the development of the spermatozoa. In the case of animals with a temporary descent of the testes there is no development of the spermatozoa while the testes are retained within the body cavity. This theory also explains the frequent sterility that accompanies cryptorchism.

B. Ovaries

Ovaries, like testes, are "glands" of double function, producing cells, or ova, and endocrine secretions that are distributed through the blood. They may have a simple attachment to the peritoneum, or be encapsuled and hang freely in the body cavity, being connected to the body wall by a *mesovarium*, homologous with the mesorchium of the testes. They may even be embedded in the peritoneum, as in the rabbit and cat.

Fig. 386. — Urogenital organs of a female bird, showing the single ovary. (After Roule.)

Asymmetrical development of the ovaries appears in some elasmobranchs, particularly rays of the families *Trygonidæ* and *Myliobatidæ*, where the right ovary is forced to make way for the intestine with its large, bulky, spiral valve. Some of the bony fishes, for example, the perch, *Perca*, and the curious little sand lance, *Ammodytes*, show a fusion of the two ovaries into one, while in *Mormyrus oxyrhynchus*[2] and some others only the left ovary develops. In birds also only a single ovary develops (Fig. 386), the left one being the one that is "left," although a few birds, such as owls, hawks, pigeons, and parrots, sometimes show remains of the lost right ovary. The reason for

[1] *Amer. Jour. of Anat.*, v. 34, 1924.

[2] Found in the Nile.

the single ovary in birds may have to do with the drastic elimination of unnecessary ballast in adaptation to flight, or possibly with the safe manipulation of the large eggs which have breakable shells. With the single ovary there is only a single oviduct remaining, but with two ovaries and oviducts it might prove disastrous if two fragile eggs at the same time should approach the narrow exit, side by side, to be laid.

The ovaries of elasmobranchs, crocodiles, turtles, birds, and mammals are more or less solid in character, and the eggs which are embedded in them dehisce through the periphery directly into the body cavity to be picked up by the open ends of the oviducts. Amphibians, lizards, and snakes have saccular ovaries that are hollow within, but the eggs still break through the outer wall, arriving by the indirect route in the oviducts.

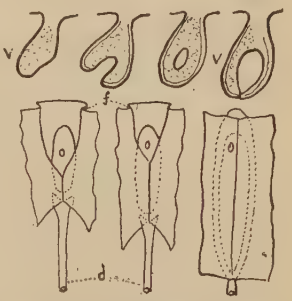


Fig. 387.—Schematic representation of the closure by the wall of the cœlome of the ovary of a teleost. The upper row represents sections; lower row, surface view. *f*, peritoneal fold; *o*, ovary; *d*, terminal duct; *v*, ventral side of sections. (After Haller.)

The ovaries of teleost fishes, which are likewise hollow, form an apparent exception. In this case the eggs collect within the ovaries and pass directly into the oviduct, that is simply an elongation of the hollow ovary without entering the body cavity at all. As a matter of fact, however, the space within the ovaries of teleosts is actually a shut-off portion of the original cœlome, as indicated by Fig. 387, which shows the manner of origin of teleostean ovaries from the embryonic genital ridge, so that here again the eggs may be said to be inducted into the body cavity on their way to the oviducts.

The garpike, *Lepisosteus*, alone of the ganoid fishes follows the teleost plan. Other ganoids have "solid" ovaries, those of *Amia* and *Polypterus* being long, irregular and bandlike.

During the breeding season the ovaries of fishes become engorged with eggs and increase enormously in size, until they may equal as much as twenty-five or thirty per cent of the total body weight.

The cavity of the saccular amphibian ovaries is lymphoid in character, and is not comparable with that of teleosts from which it differs fundamentally in origin, its lumen having been hollowed

out secondarily instead of representing a portion of imprisoned cœlome.

In turtles the ovaries are symmetrically disposed, but asymmetry in position appears in the lizards and becomes quite pronounced in snakes, with the right ovary placed in advance of the left.

The ovaries of the duckbill, *Ornithorhynchus*, owing to the few large projecting eggs which they contain, are somewhat lobulated, "resembling a bunch of grapes," while those of most other mammals are relatively small, round, and smooth in contour, being enveloped in a dense layer of fibrous tissue, the tunica albuginea. Underneath this layer is the *cortex*, which is the general seat of the ova, while the interior constitutes the *medulla*, or vascular region of the ovary.

C. Hermaphrodites

By far the greatest number of vertebrates are *diœcious*, that is, the ovaries and testes are borne by different individuals. There are a few instances, however, of *hermaphroditism*, when the two sexes are combined in a single individual, a condition common among certain invertebrates, which, by reason of isolation, or absence of locomotor organs, need to overcome the difficulties attendant upon pairing.

For example the sea bass, *Serranus scriba*, is regularly hermaphroditic and self-fertilizing, while another exceptional teleost, *Chrysophrys auratus*, is a proterandrous hermaphrodite, being first male and afterwards female.

The unpaired gonad of the hagfish, *Myxine*, appears at times to produce sperm, and at other times, eggs, while the larval "Ammocœtes" form of the lamprey eel, according to Lubosch, shows hermaphroditic gonads in twenty-five per cent of the cases.

Occasional cases of hermaphroditism have been observed in the codfish, mackerel, and herring among bony fishes, as well as in the Alpine newt, *Triton*, and in frogs and toads among amphibians.

So-called instances of human hermaphrodites, cited in medical literature, usually concern abnormalities of the external genitalia rather than the functional gonads. It is extremely doubtful whether there is any authentic case on record of a human being that has produced both eggs and sperm, for the evidence in supposed instances is likely to be extremely obscure.

D. Gametogenesis

The fertilized egg of any vertebrate, when it is ready to develop into a new individual, is essentially germplasm, but by a succession of mitoses the original cell soon becomes many cells from which the somatoplasm, or the body of the individual, is elaborated. Somewhere early in the preliminary cell divisions there comes a parting of the ways between reserve germplasm and somatoplasm, whereby one of the two daughter cells in a mitotic division is set aside to carry on the traditions of the race, while the other proceeds in the service of the developing individual (Fig. 380). Each of these two ancestral cells, particularly that of the somatoplasmic line, undergoes countless subsequent mitoses, but their descendants differ fundamentally. The germplasmal line eventually becomes eggs and sperm, with the innate possibility of giving rise to new individuals, while the somatoplasmal line differentiates into the specialized tissues of the body from which, like a blind alley, there is no return to primitive potentialities.

The reserved germplasmal cells find their way to the gonads where they hold their own unchanged until puberty, that is, the time when the individual arrives at sexual maturity. They then resume activity and go through a series of preparatory changes that make them into mature sperm and eggs, fit for fertilization or union. This is the process of gametogenesis (*gamete*, marrying cell; *genesis*, origin).

The essential process in the final differentiation of sexual germ cells, is the elimination of half of the chromosomal material, bearing the hereditary determiners, from the nucleus of the egg and sperm, so that, upon the union of the two germ cells, the number of chromosomal units proper and characteristic for the species in question, will be restored. If this reduction of chromosomes did not occur before the fertilization of the egg, there would be a doubling of the chromosomes in each generation, which would quickly upset the machinery of mitosis.

The transformation of *spermatogonia*, or ancestral sperm cells, into mature locomotor sperm, occurs in the walls of the tubuli contorti within the testes (Fig. 382). The genital ridge between the Wolffian body and the mesentery on either side within the body cavity, is composed of a mass of mesodermal cells that form the testes, with the cells on the outside facing the cœlome arranged in a layer of epithelium. In this superficial layer certain germ-

plasmal cells give rise, by repeated divisions, to special, cordlike, cellular masses which push down into the undifferentiated cells of the testis. These solid cellular strands later become hollowed out and enormously elongated to form the *tubuli* of the testis, in the walls of which are lodged the spermatogonia.

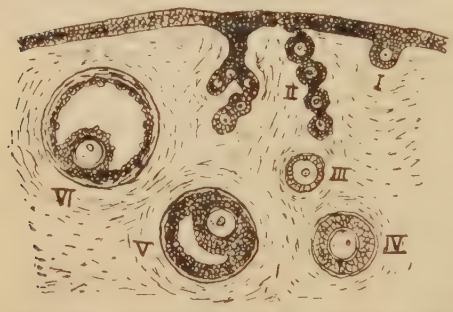


FIG. 388.—Oögenesis. The genesis of the ovum, within the Graafian follicle in the ovary, is indicated by the successive numbers *I–VI*, (After Boule.)

With some notable differences, *oögenesis*, or the origin of the egg, is a similar process to *spermatogenesis* or the origin of the sperm. The ovary develops from the genital ridge in the female, with an outer stratification of epithelium in which are certain germplasmal cells that proceed to proliferate as cellular masses, *Pflüger's cords*, down into the substance of the ovary (Fig. 388). These cords, however, do not hollow out, as do the corresponding structures in the developing testis, but form "follicles" instead. Each follicle is characterized by the presence of a central primary cell, or *ovum*, surrounded by numerous secondary *follicular cells*, which later may be sacrificed as nutriment for the cannibalistic egg cell within.

FIG. 389.—Ovary of a girl 19 years old, who died suddenly eight days after menstruation, showing the *corpus hæmorrhagicum*. (After Kollmann. From Anatomical Collection in Basel.)

In mammals the follicular mass, or *Graafian follicle*, becomes hollowed out and filled with fluid so that the developing ovum is practically surrounded by a double wall of follicular cells. The Graafian follicle migrates as a whole from its embedded position and gradually crowds to the surface of the ovary, where it bulges out as the fluid-filled cavity increases in size, and eventually it ruptures, thereby extruding the egg into the cœlome.

The cavity of the ruptured Graafian follicle immediately be-

comes filled with a blood clot, the *corpus hæmorrhagicum* (Fig. 389), which is gradually invaded and replaced by peculiar yellow *lutein cells*. This periodically recurring mass of cells has an endocrine function, and will be referred to again in the following chapter.

Eventually the *corpus luteum*, formed by the lutein cells, is obliterated by the growth of connective tissue, leaving a scar on the surface of the ovary, the *corpus albicans*, which is all that remains to tell the story of the origin of a mammalian egg.

Successive phases of the development and rupture of the Graafian follicle in the mammalian ovary, are shown in Fig. 388.

2. Ducts

A. Disposal of Gametes

Upon maturity the sex cells are naturally shed into the cœlome, since the gonads are a part of the inner wall of this cavity which may be regarded as an expanded gonadal sac.

There are at least three general ways among vertebrates by which the mature gametes finally escape to the outside, namely: (1) through pores, no ducts being present; (2) through ducts continuous with the gonads; and (3) through ducts not continuous with the gonads and for the most part taken over from the mesonephridial system.

The first of these avenues of escape is seen in amphioxus, whose gametes are extruded into the peribranchial chamber and thence out through the *atrial pore*, and in some cyclostomes, which receive eggs and sperm in the body cavity whence *abdominal pores* furnish an exit into the urogenital sinus behind the anus (Fig. 366). These pores are usually paired or may present a single opening through a papilla, as in *Petromyzon*.

The method of disposal of sex cells through abdominal pores is also utilized in *Amia* and *Lepisosteus* among the ganoids, and in a few teleost fishes, for example, in the smelt, *Osmerus*, and the salmon, *Salmo*. Here, however, it is evidently a degenerate condition, for two short, imperfect ducts, focusing at a single abdominal pore, project into the body cavity.

Teleost fishes present the second category of germ-cell disposal, that is, by means of direct ducts connected with the gonads (Fig. 387). In these animals the sex cells never enter the body cavity but pass out directly through ducts formed by an elongation of

the hollow gonads, or by peritoneal folds that entirely invest the gonads. In most cases the sex ducts join posteriorly with the urinary ducts, and open behind the anus.

The third method, that is, of indirect ducts, is by far the most prevalent. In elasmobranchs, dipnoi, amphibians, reptiles, birds, and monotremes, the ducts open into a cloaca (Fig. 367), but in mammals other than the monotremes, directly to the outside (Fig. 371). In males generally of this third group, the sperm, never entering the body cavity, reach the sperm duct indirectly after passing through the epididymis. In females, on the other hand, the eggs do enter the body cavity from the ovary and are then picked up by the open ends of the unconnected oviducts for transference to the outside. There is thus a fundamental difference in the disposal of the germ cells of the two sexes.

B. Origin of the Genital Ducts

Exclusive of the teleosts there is an intimate relation, particularly in the male, between the ducts that dispose of the sexual products and the mesonephridial system. It will be remembered that the pronephric, or segmental, ducts of the pronephroi remain after the pronephridia have been replaced by mesonephridia, to become the mesonephric or Wolffian ducts (Fig. 367). These ducts not only drain the mesonephros, but, in the case of male elasmobranchs and amphibians, they also serve as sperm ducts and are, therefore, properly designated as *urogenital ducts*.

The connection of the urogenital ducts with the testes is accomplished through the mesonephridia in the anterior part of the mesonephros, which is accordingly termed the "sexual kidney," or *epididymis*, in distinction from the posterior part, or "urinary kidney."

In male reptiles, birds, and mammals, only the sexual kidney remains functional as the epididymis, while the urinary part of the mesonephros, being replaced by the permanent kidney, or *metanephros*, becomes degenerate (Fig. 371). The Wolffian ducts, however, persist as sperm ducts exclusively, now being termed *ductuli deferentes*, the urinary products of the metanephros being disposed of through the newly formed ureters.

The oviducts are less directly related to the mesonephridial apparatus. Early in embryonic life a second duct, the *Müllerian duct*, appears alongside the Wolffian duct (Fig. 367). This be-

comes the oviduct. It may form by longitudinal splitting of the Wolffian duct, as in elasmobranchs and some amphibians, or it may develop parallel to the Wolffian duct out of surrounding tissues, either as a groove in the peritoneum that becomes closed off, or as a solid strand of cells that afterwards becomes hollowed out.

The open end of the Müllerian duct, or the *ostium abdominale*, in the case of elasmobranchs and some amphibians, is probably derived from a persistent nephridium that has attained embryonic connection with it (Fig. 365, B). Thus the ostium abdominale, into which the ova from the body cavity enter, is homologous with the nephrostome of a nephridium which ancestrally served to drain the body cavity of fluids of excretion. In other vertebrates there is no connection, either in the male or female, between the embryonic Müllerian duct and the urinary apparatus, and the ostium abdominale is formed as the remains of the peritoneal groove that made the Müllerian duct. In mammals the Müllerian duct gives rise not only to the oviducts but also to the uterus and vagina.

In the male the Müllerian ducts are also present embryologically, but in the adult they usually suffer various degrees of degeneration. The lungfish, *Neoceratodus*, and the newt, *Triton*, as well as the leopard frog, *Rana pipiens*, are exceptional cases showing persistent Müllerian ducts in the adults of male animals.

C. Sperm Ducts

After leaving the walls of the *tubuli contorti*, the sperm cells pass through the *tubuli recti* and the *rete testis*, emerging into the *epididymis* (Fig. 384). This is essentially an organ made up of several *ductuli efferentes*, and a very much coiled proximal part of the Wolffian duct, the *ductus epididymidis*. In reptiles the epididymis is sometimes a larger structure than the testis itself.

The ductuli efferentes are transformed mesonephridia which have lost their glomeruli and acquired a connection with the rete through so-called *junctional cords* of cells that later become hollowed out. In man the ductuli efferentes, of which there are from nine to fifteen in each epididymis, are very much coiled, and together form the *globus major* of the epididymis. They still empty into the end of the Wolffian duct as they did when they were mesonephridia before they were converted into ductuli efferentes

and transferred to the service of the reproductive system. This end of the Wolffian duct is also greatly convoluted and constitutes a mass known as the *globus minor* of the epididymis. From the globus minor the Wolffian duct emerges as the *ductus deferens*. The entire Wolffian duct in man, according to Lewis, is about twenty feet in length when straightened out.

Near the larger open end of the Wolffian duct there is usually a saccular expansion called the *seminal vesicle* (Fig. 381), which is glandular in character, rather than a temporary storage place for the sperm as its name would indicate.

In mammals the urethra joins the ductus deferens beyond the point where the seminal vesicle opens into it, so that the end of the sperm duct in an amniote, like the entire duct in the males of elasmobranchs and some amphibians, is urogenital in character and serves the double function of disposing of both sperm and urine.

That part of the ductus deferens between the seminal vesicle and the point of junction of the ductus deferens and urethra, is termed the *ejaculatory duct* (Fig 381).

D. Oviducts

Embryologically the oviducts are Müllerian ducts which arise, as already indicated, either by splitting off from the Wolffian duct (elasmobranchs and some amphibians), or independently of the nephridial apparatus by the closing over of the peritoneal groove, or the hollowing out of a cord of cells lying parallel to the Wolffian duct (most vertebrates).

Fig. 390.—Urogenital apparatus of a female reptile. (After Roule.)

Each oviduct, with the exception of those of teleosts, opens freely into the body cavity by an ostium abdominale (Fig. 390). This may be located at some distance from the ovary itself and the point where the eggs dehisce, or it may close around the ovary, as in man, so that, while the eggs theoretically pass through the body cavity, there is little chance that they escape therein and miss the opening of the oviduct. Once within the oviduct the eggs are forwarded by peristalsis of the muscular walls.

In teleosts, as already indicated, there is an organic unity between the ovary and the oviduct, entirely preventing any ex-

cursion of the egg into the cœlome, and in some carnivores, as, for example, the walrus and the seal, the ovary becomes so encapsuled within the lips of the ostium abdominale, that it superficially resembles the condition in teleosts.

In some elasmobranchs the open ends of the two oviducts are fused together, forming a single ostium. There is also coalescence of the proximal ends of the oviducts in marsupials. Fusion at the cloacal, or distal, ends of the oviducts, however, is more common. It usually occurs in teleosts and some anura, as well as quite extensively among mammals.

Fig. 391. — Urogenital apparatus of a female amphibian, showing much convoluted oviducts. (After Roule.)

In those animals which produce many eggs at one time, as the frog, for example, the oviducts become enormously elongated and convoluted during the egg-laying season (Fig. 391).

The oviducts of higher vertebrates, near their exit, undergo extensive modification into uterus and vagina which will be considered later.

3. Apparatus for Effecting Fertilization

A. Fertilization in Animals and Plants Contrasted

Fertilization, or the union of egg and sperm, initiates the life history, though not the life, of a new individual. Among plants, the traveling male gamete, carried in the *pollen cell* on its way to the female gamete within the *ovule*, usually takes the air route, or steals a ride upon some accommodating insect that acts the part of matchmaker.

These methods are not employed, however, in the fertilization of the eggs of animals. The sperm cell in the case of all vertebrates goes forward in its search for the ovum, by means of a vibratile tail that requires a fluid medium in which to be effective. Naturally the problem is least complicated in the case of those vertebrates that find themselves in water when the germ cells are extruded from the body, since a suitable medium for the locomotion of the sperm is then ready at hand. When, in the course of evolution, emergence upon the land is effected the reproductive

apparatus has to be profoundly supplemented in order to accomplish fertilization successfully.

It is evident that the sperm of non-aquatic animals are compelled to encounter the eggs while they are still within the body of the female, since sperm cells cannot locomote through the air. This necessitates the pairing of the sexes by actual contact, so that the sperm may be definitely placed within the oviduct, rather than the promiscuous broadcasting of germ cells followed by chance union, as in aquatic vertebrates. Moreover, a fluid, indispensable for the lashing tails of the locomotor sperm cells, must be elaborated from special glands provided for the purpose, in order that the distance within the oviducts between the entering sperm and the descending ovum, may be successfully covered.

Whenever internal fertilization occurs, the egg may either be provided with a protective shell and laid, afterwards to be incubated and hatched (*oviparous animals*), or it may undergo its preliminary development within the sheltering walls of the female body before venturing alive into the world (*viviparous animals*).

To insure the placement of the sperm within the oviduct, various holdfast mechanisms, as well as organs of copulation, have been evolved by different animals.

B. Holdfast Mechanisms

The Amphibia, which are halfway land animals, have been so occupied with adapting themselves to a dual existence that they have not been able to accomplish much in an evolutionary way for their reproductive apparatus. The result is that, for the most part, they return to the water during the breeding season, where a fluid for the locomotion of the sperm cells is provided, and there is no necessity for elaborating organs to accomplish internal fertilization.

Amphibians do, however, improve somewhat upon the improvident wasteful ways of fishes, with their countless eggs and unthinkable numbers of sperm. For example, frogs practice *amplexation* during the breeding season (Fig. 31, B), that is, the male frog saddles himself upon the back of the female, whose body, unfettered with hooplike ribs, becomes more and more swollen by the increasing mass of eggs within. The male retains his grasp upon the back of the slippery female by means of temporarily swollen, glandular

thumbs (Fig. 392), which are inserted under the armpits of the female and act as holdfasts. He remains in amplexation until the female extrudes the eggs, when he immediately sheds the sperm over them. In this way the hazards and uncertainties of distance between the germ cells of the two sexes are greatly lessened.

The hylas, or tree frogs, and the "obstetric frog," *Alytes*, of Europe, do not ordinarily resort to the water to breed, but Kammerer reports that when *Alytes* is compelled to breed in water, amplexation occurs and the thumbs of the male become swollen and roughened.

Fig. 392.—Right fore foot of a male frog, *Rana esculenta*, showing the epidermal swelling on the radial side, which appears temporarily during the breeding season, and is an aid in grasping the female securely during amplexation. (After Leydig.)

Many male lizards possess a row of peculiar porthole-like "glands" down the inner surface of the hind legs (Fig. 140). These femoral structures are not true glands with a liquid secretion, but they extrude a dry scaly substance that roughens the surface, so that when the male lizard in mating grasps the female between his hind legs, the security of his grip is insured.

Snakes coil around each other in the mating embrace, and the male boa constrictor, according to Boaz, is supplied with *anal hooks* that aid in holding together the cloacas of the two sexes.

Among higher vertebrates, organs already present but not especially evolved to accomplish the holdfast function in reproduction, are utilized for this purpose. Thus, the cock, when treading a hen, employs his beak and claws.

In animals like ruminants, where there are no holdfast organs, the sexual act is usually accomplished very quickly, as in the case of the almost instantaneous leap of the stag.

C. Male Copulatory Organs

Copulation consists in the introduction of a male copulatory organ, the *penis*, through which the sperm duct is extended, into the modified end of the oviduct, or the *vagina*. The discharge of the sperm cells under these circumstances makes more certain their placement in the immediate vicinity of the eggs to be fertilized.

It is quite to be expected that the apparatus for copulation in the aggressive male with sperm cells to deliver, should be

more complicated than that of the receptive female, and such is the case.

Not all the organs of copulation among vertebrates are homologous. Thus, male elasmobranchs in many species possess a pair of grooved "claspers," one on each side of the cloaca, which are modifications of the medial parts of the pelvic fins (Fig. 393, A). In these animals, whose young are "born alive" in an advanced stage of development, copulation and internal fertilization are effected by the aid of these claspers which are inserted into the cloaca of the female and serve to direct the sperm along their grooved inner margins into the oviducts (Fig. 394).

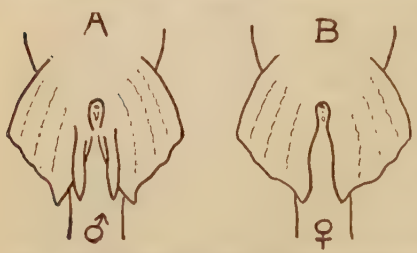


FIG. 393.—Cloacal region of (*A*) male and (*B*) female dogfish, showing the *claspers* of the male. (After Jammes.)

Rarely among teleosts also is found a similar contrivance that serves as an intromittent organ. It is formed sometimes out of the ventral or anal fin, as in the strange Brazilian viviparous bony fish, *Girardinus*, and sometimes even from the metamorphosed hæmal spine of a caudal vertebra.

It is with life on land, however, that the evolution of internal fertilization, and the attendant copulatory mechanisms really begin, although none of the amphibians have a penis, with the possible exception of the footless cæcilians (Apoda), that have largely taken to land life in damp situations in the tropics. In these animals the walls of the male cloaca at copulation are everted into the cloaca of the female, thus serving as an intromittent structure.

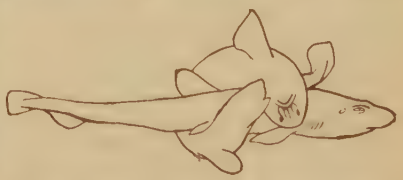


FIG. 394.—Dogfish in copulation. (After Bolau.)

Internal fertilization without the assistance of copulatory organs, is effected among certain urodeles, *Triturus*, *Ambystoma* and *Triton*, for example, by the circumstance that the males during the breeding season deposit their sperm in small compact packets, *spermatophores*, surrounded by a protective gelat-

inous mass. The females follow after the males as they produce the spermatophores and pick them up with their cloacal lips.

Among modern reptiles there are evolved two types of penes. First, lizards and snakes possess double cloacal organs which may be everted, somewhat after the manner employed by the cæcilians. Each *hemipenis* has a spiral groove along its medial surface for the conveyance of the sperm. Second, turtles (Fig. 395, A), and crocodiles have a single penis, lying on the ventral wall of the cloaca, slightly protrusible and supplied with erectile tissue, with a dorsal groove along its length. During copulation this groove is made into a temporary canal by the application of the organ against the upper dorsal wall of the cloaca. The single penis in the crocodiles at its base is formed of two component parts, suggesting a double origin. In turtles the size of the penis bears a direct relation to the difficulties encountered in copulation because of the awkward shell, being smaller in marine turtles having a flattened or incomplete plastron, than in fresh water or land forms with a more complete and projecting shell.

Among birds there is no true copulation, but impregnation by the method of the cloacal kiss is the general rule. There are, however, a few birds, notably the ostriches and other ratitates, certain ducks, and the South American "tinamou," *Tinamus*, which have well developed penes, resembling those of crocodiles.

The penis in all mammals, with the exception of the monotremes (Fig. 395, B), is a closed tube and not a grooved structure as in the reptiles. It is typically a turgescent organ, under the control of vasodilator nerves which arise as automatic fibers in the sacral region of the spinal cord, and is composed of two masses of erectile tissue side by side, the *corpora cavernosa penis*, with a third similar mass, the *corpus spongiosum* beneath them, held together by fibrous tissue and enveloped by a layer of loose skin. The corpus spongiosum is perforated for its entire length by the urethra. Consequently the urethra is considerably longer in the male than in the corresponding female, and it terminates in an enlargement of the penis called the *glans* (Fig. 381).

In some animals, as for example, the guinea pig and wombat, the glans is beset with horny recurrent spines, or corneous scales,

although in most cases the skin extending over its surface is extremely sensitive and without any corneal layer. Ruminants, cetaceans, cats, and some rodents are exceptional, in that there is no glans present, while sheep, goats, and many antelopes,

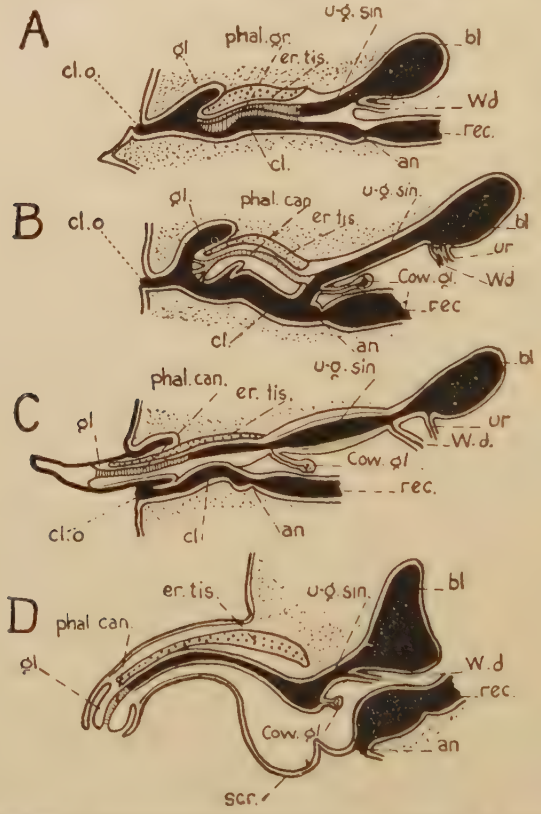


FIG. 395.—Stages in the evolution of the penis. *A*, tortoise; *B*, spiny anteater; *C*, kangaroo; *D*, man. *an.*, anus; *bl.*, bladder; *cl.*, cloaca; *cl.o.*, cloacal opening; *Cow.gl.*, Cowper's glands; *er.tis.*, erectile tissue; *gl.*, glans; *phal.gr.*, phallic groove; *phal.can.*, phallic canal; *rec.*, rectum; *u.g.sin.*, urogenital sinus; *ur.*, ureter; *W.d.*, Wolffian duct; *scr.*, scrotum. (After Keith.)

possess a peculiar, threadlike elongation of the sperm duct beyond the end of the penis itself, called the *processus urethralis* (Fig. 396). Among higher mammals the glans is enveloped in a double fold of skin, the *preputium* (Fig. 381).

In the case of several kinds of mammals, namely, marsupials,

cetaceans, carnivores, rodents, bats, monkeys, and some apes, there is present in various degrees of development, lying between the two corpora cavernosa and above the urethra, a penis bone, *os priapi*, which increases the rigidity of the intromittent organ.

In mammals the obliteration of the cloaca goes hand in hand with the evolution of the penis (Fig. 395). In the monotremes there is still a cloaca present and the small non-protrusible penis is enclosed in a sac between the urogenital sinus and the cloaca itself. It is a fibrous, slightly erectile structure of double origin, with a groove between the two parts that is converted into a canal, except posteriorly where the urogenital and cloacal passages still connect with each other. The ureters do not terminate in the bladder with a urethral outlet for the urine, but directly into the cloaca, and the penis is utilized solely for the passage of the sperm. The marsupial penis, with the reduction of the cloaca, becomes an external erectile structure directed backward, through which both urine and sperm have common passage-way, as in all higher mammals. The scrotum with the testes is located anterior to the penis, which is directed backward. The distance between the penis and the anus in marsupials is so slight that they are enclosed together within a common muscular sphincter. The opossum *Didelphys*, the bandicoot *Perameles*, and some others, have a bifurcate glans that is probably correlated with the double vagina in the females of these forms.

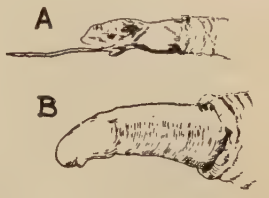


FIG. 396.—*A*, distal end of ram's penis, showing glans and filiform appendage. *B*, distal end of bull's penis, showing glans and urethral papilla, representing vestigial filiform appendage. In both cases the prepuce is folded back. (After Marshall.)

Among placental mammals the penis is in front of the scrotal sac, and usually withdrawn within a protective sheath, except during sexual activity. In most cases it is directed forward, and, when no sheath is present, is pendulous, as in bats and man. In monkeys and apes it is partly pendulous and partly ensheathed. In cats and rodents it is directed backward, except during copulation, so that these animals micturate posteriorly. Armadillos, handicapped by their awkward armor, have a relatively enormous penis which may extend as much as one third the length of the body during copulation.

D. Female Genitalia

The female genitalia concerned in copulation, aside from certain glands and the rudimentary clitoris, are the vagina, vestibule, hymen, and the labia minora and majora (Fig. 397). All these structures are differentiated to an extent similar to the degree of evolution attained by the copulatory organs of the corresponding males, reaching their maximum in the primates.

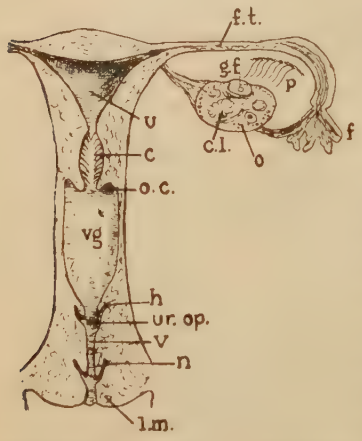


Fig. 397.—Diagram of human female reproductive organs. *o*, ovary; *g.f.*, Graafian follicle, containing an ovum; *c.l.*, corpus luteum; *p*, parovarium; *f*, fimbriated end of Fallopian tube; *f.t.*, Fallopian tube; *u*, body of uterus; *c*, cervix of uterus; *o.c.*, os cervix; *vg.*, vagina; *h*, hymen; *ur.op.*, urethral opening; *v*, vulva; *n*, labia minora, or nymphæ; *l.m.*, labia majora. (After Henle and Symington.)

The *vagina* is that part of the oviduct adapted to receive the penis. It is absent in the monotremes where the cloaca serves the same purpose. In the opossum, *Didelphys*, and other marsupials there are two distinct vaginas which barely coalesce into one at the outer end or entrance, while in some other marsupials there is also a coalescence at the inner ends from which a median diverticulum, or third vagina, extends backward as a blind alley between the two lateral vaginas (Fig. 398). Whenever a fetus becomes deposited in this middle closed vagina, instead of in one of the two lateral open passage-ways, there is a rupture at birth at the blind end of the middle vagina to allow for the expulsion of the young.

In placental mammals the outer ends of the two oviducts fuse together to form a single vagina (Fig. 399), located between the rectum, dorsally, and on the ventral side, between the bladder and the urethra. It is lined with mucous membrane, and frequently presents transverse rugæ, particularly in young females. The vaginal mucosa is without glands, the mucus present coming from the walls of the uterus which is continuous with the vagina higher up. The walls of the vagina are muscular and collapsible, and the circular muscle fibers near the external orifice form a sphincter.

The outer part of the vagina constitutes the *vestibule*, which in man is separated from the vagina proper by a temporary fold of mucous membrane, more or less complete, the *hymen*, that partially occludes the passage-way, particularly before copulation has taken place. The walls of the vestibule are supplied with some erectile tissue which may become upon occasion surcharged with blood.

In primates generally around the vestibule on either side are two folds of skin, the *labia minora*, while in the higher primates there are in addition two larger external folds, covered outwardly with hair, and supplied with a certain amount of fatty tissue, the *labia*

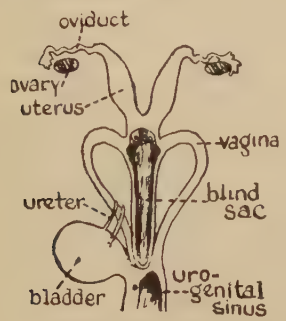


Fig. 398. — Female sexual apparatus of Kangaroo, showing the double vagina. (After Gegenbaur.)

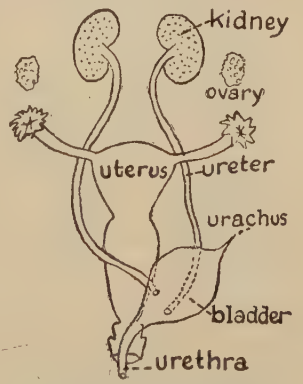


Fig. 399.—Urogenital apparatus of female mammal. (After Roule.)

majora. There is also a pad of adipose tissue above the vestibular orifice at the edge of the pubic bones, that is likewise covered with hair, called the *mons Veneris*, which is better developed in the human females of civilized races than in those of more primitive types. The female Hottentot is remarkable for the hypertrophy of the labia minora, as well as of the gluteal muscles behind, resulting in enormously fat buttocks, or *steatopygy* (Fig. 400).

The *clitoris* in the female is homologous with the penis in the male, and it is situated above the vestibular opening between the folds of the labia minora. It consists of two corpora cavernosa and is erectile, but there is no corpus spongiosum present, and it is not traversed by a urethra, as is the male penis, except in a few rodents, insectivores, and lemurs. In this latter case the urethra is not a urogenital canal, as in the male penis, but is exclusively for the

transmission of the urine. An imperforate clitoris is present in turtles and crocodiles, and in those few birds whose males possess a penis. There is even a clitoris bone in certain mammalian species to correspond to the *os priapi* of the male. The clitoris is relatively large in monkeys, being six to seven centimeters long in a young spider monkey, *Ateles*, but in the human female it is small and degenerate.

FIG. 400.—Female Australian bushman, showing steatopygy. (From Martin after a photograph by Schulze.)

4. Accessory Glands

Associated with the reproductive apparatus are various glands which (1) provide a fluid medium for the locomotion of the sperm cells; (2) facilitate copulation by reducing friction; (3) produce odors that are stimulative to the opposite sex; (4) furnish nutriment to the developing young. These glands may be grouped according to their place of origin into those originating (1) in the sperm duct, or oviduct; (2) from the urogenital canal; or (3) in the integument.

A. Originating in the Sperm Duct, or Oviduct

In many cases, as for example, ruminants, most rodents, dogs, bears, martins, and shrews, the outer end of the sperm duct enlarges into an "ampulla," which serves as a temporary reservoir for the sperm. This is lined with *ampullar glands* which secrete mucus. These glands are absent in the cat, mole, pig, and the European hedgehog, *Erinaceus*. Also at the end of the sperm duct in most mammals, there is a pair of saclike *seminal vesicles* (Fig. 401), that are lined with mucous glands and exercise a glandular rather than a storage function, although sperm cells are frequently found therein. In the case of bats and some mice, the seminal vesicles enable these animals to exercise a sort of "birth control," in that after copulation the mucus which they produce forms a gummy plug that fills the entrance to the uterus and prevents for a considerable time subsequent impregnation. There are no seminal vesicles in monotremes, marsupials, cetaceans, or carnivores. In man the seminal vesicles appear first as tubular diverticula about the end of the third month of fetal life.

In the human female there are present at least three sorts of glands, namely, uterine, cervical, and vestibular, associated with corresponding regions of the oviduct.

The *uterine glands* are tubular structures lining the uterus. They have to do with the epithelial regeneration of the uterine walls during menstruation, rather than with glandular secretion. The much-branched *cervical glands*, which surround the neck and mouth of the uterus, produce mucus that moistens the inner surface of the glandless vagina, and the scattered *vestibular glands*, located near the clitoris in the vestibule and around the outlet of the urethra, perform a similar function.

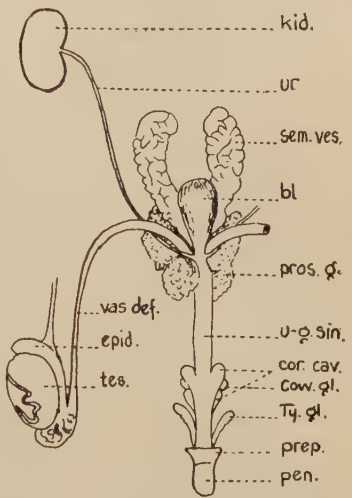


FIG. 401. — Urogenital apparatus of a hamster, *Cricetus*. *bl.*, bladder; *cor.cav.*, corpora cavernosa; *Cow.gl.*, Cowper's glands; *epid*, epididymis; *kid.*, kidney; *pen.*, penis; *prep.*, prepuce; *pros.g.*, prostate gland; *sem.ves.*, seminal vesicle; *tes.*, testis; *Ty.gl.*, Tyson's glands; *u.g.sin.*, urogenital sinus; *ur.*, ureter; *vas.def.*, ductus deferens. (After Gegenbaur.)

B. ORIGINATING FROM THE UROGENITAL CANAL

The glands of the urogenital canal are the prostatic in the male only, and the urethral glands, which appear in both sexes.

The *prostate gland* (Fig. 381), in man at least, is the most important of all the accessory reproductive glands. It is a compound tubuloalveolar gland of thirty to fifty lobules, opening into the urethra by means of two large and fifteen to thirty lesser ducts. It is embedded in connective tissue and abundantly supplied with blood, nerves, lymph, and more smooth muscle fibers than any other gland. It surrounds the base of the urethra at the point where it leaves the bladder, and is enclosed in a tough capsule. The secretion produced by the prostate gland, forming a large part of the spermatic fluid is a thin, milky emulsion, faintly acid, and with a characteristic odor. The prostate gland is well developed in rodents, bats, perissodactyls, primates, and most carnivores. It is less developed in ruminants, and is absent in monotremes, marsupials, edentates, and, among car-

nivores, in the martin, otter, and badger. In man the prostate gland frequently becomes hypertrophied in old age, and may deposit concretions of calcium phosphate, causing trouble by pressure upon the urethra which it envelops.

The urethral glands are of two sorts: first, mucous glands along the urethra (*glands of Littré*), that are most numerous in the dorsal region of the urethral wall in the penile part of its course and are particularly characteristic of the male; and second, a pair of "bulbo-urethral glands" (*Cowper's glands* in the male and the *glands of Bartholini* in the female). Cowper's glands, two small structures about the size of peas in man, with ducts an inch and a half long opening into the urethra at the base of the penis, produce a clear, glairy mucus during sexual excitement. They are always present in mammals, with the possible exception of bears and dogs, and are especially large and active in rodents, elephants, pigs, camels and horses. The male *Echidna* has no other accessory reproductive glands.

Corresponding to Cowper's glands in the male, are the glands of Bartholini in the female, that open into the vestibule in the groove on either side between the hymen and the labia minora. They produce mucus which functions largely as a lubricant during copulation.

In the formation of the spermatic fluid, it has been shown by Szymonowicz that the first contributions come from Cowper's glands and the glands of Littré. This is followed by the secretion of the prostate gland before the sperm are added from the ductus deferens, while the last contribution is from the seminal vesicles.

C. Originating in the Integument

Various odoriferous glands of integumental origin, named in different cases, *anal*, *inguinal*, *perineal*, and *cloacal glands*, occur among vertebrates. These are usually located around the anus or the genital aperture, and serve to stimulate the opposite sex. The famous scent glands of skunks belong to this category, as do also the anal glands of dogs, which are well known to be of paramount social importance to these animals. *Tyson's glands* are small sebaceous glands that are situated at the base of the glans on the penis in the depths of the preputial fold of skin. They also produce an odorous substance. The male alligator has a *submaxillary gland* at the edge of the lower jaw on either side, which enlarges

and emits a musky odor during sexual excitement. Finally, under integumentary glands there should be mentioned the *mammary glands*, already described in a previous chapter, that have a place in the general scheme of reproduction in the mammals, since they provide sustenance for the newly born young.

Marsupials, which have no true placenta, nourish the fetus before birth with "uterine milk" produced by uterine glands.

5. Devices for the Care of the Eggs and Young

A. Uterus

With most animals that practice internal fertilization, a part of the oviduct becomes modified into a brood organ, the *uterus*, for the protection of the developing embryo. This structure is located midway between the upper portion of the oviduct, called in man the *Fallopian tube*, which receives the egg from the ovary, and the vagina below. It is usually considerably enlarged and has thick, muscular walls capable of great distension. When unoccupied by young, the cavity within the uterus is relatively small, and the inner walls are more or less in contact with each other. The mouth of the uterus where it meets the vagina frequently projects somewhat into the vaginal cavity (Fig. 397).

In higher mammals the walls of the uterus undergo marked periodic modification throughout sexual life, except when interrupted by pregnancy, which results in the eventual disintegration and sloughing off of the superficial layer of mucosa, together with a certain amount of blood, and the subsequent repair of the uterine lining. This process is termed *menstruation*, and it is more or less synchronous with the bursting of the Graafian follicle in the ovary and the extrusion of the egg. If the descending mammalian egg is fertilized by an ascending sperm cell, it may become implanted in the wall of the uterus and there undergo fetal development.

Even in frogs the oviduct during the breeding season enlarges at its cloacal end into a uterus for the temporary lodgment of the eggs, and viviparous teleost fishes, as also some elasmobranchs, have a well developed uterus, although mammals show the greatest differentiation of this organ.

In lower vertebrates which possess a uterine modification of the oviduct, it is usually a double structure, one for each oviduct, but with the increasing coalescence of the oviducts in

mammals to form a single vagina, there is a tendency for this fusion to involve either a part or all of the uterine region. All the theoretical intermediate evolutionary stages from a double uterus to a single one, have their actual counterparts in nature among mammals.

Thus, there are two distinct uteri (*uterus duplex*, Fig. 402, A), without vaginas in monotremes, and each with a vagina in marsupials. Among placental mammals some rodents, for example,

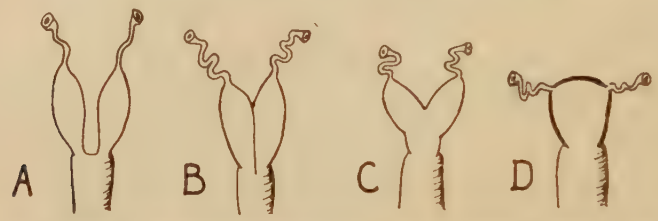


FIG. 402.—Diagrams to show the evolution of the simplex uterus. *A*, uterus duplex; *B*, uterus bipartitus; *C*, uterus bicornis; *D*, uterus simplex. (After Weber.)

the mouse, hare, marmot, and beaver, as well as elephants, certain bats, and the "aard-vark," *Orycteropus*, of South Africa, also have a duplex uterus.

A beginning of coalescence between the two uteri (*uterus bipartitus*, Fig. 402, B), is apparent in pigs, cattle, certain rodents, bats, and carnivores.

A two-horned uterus (*uterus bicornis*, Fig. 402, C), is characteristic of ungulates, cetaceans, insectivores, and some carnivores, while a single uterus (*uterus simplex*, Fig. 402, D), with two horn-like Fallopian tubes projecting from it, is the type to be seen in apes, and man.

Various pathological anomalies that suggest doubling are encountered in the human uterus, which find a ready explanation in the story of the comparative anatomy of this organ.

In the unusual South American teleost, *Girardinus*, already mentioned as having a metamorphosed hæmal spine of a caudal vertebra for a copulatory organ, the hollow ovary itself serves as a uterus, or brood sac, for the young. The eggs which dehisce into the cavity of the ovary after the teleostean tradition, are fertilized in place by sperm that penetrate all the way into the ovarian cavity.

B. Brood Sacs

There are various somewhat exceptional cases among vertebrates of brood sacs for eggs or young, aside from the uterus of the female. For example, among fishes there is a brood sac on the ventral side of the male pipefish, *Sygnathus*, in which the eggs are deposited by the female. In the sea horse, *Hippocampus*, a relative of the pipefish, there is a similar arrangement whereby the male becomes responsible for the care of the eggs (Fig. 19, A).

Among amphibians there is a dorsal pouch on the back of the female frog, *Nototrema pygmæum*, of Venezuela, for carrying the eggs (Fig. 31, F), and the male of *Rhinoderma darwini*, of Java, transforms his vocal sacs temporarily into brood pouches (Fig. 31, H).

The transient brood sac of the monotremes, and the permanent "marsupium" of the marsupials among mammals, are further examples of structures belonging to the reproductive apparatus, since they obviously have been developed in the interests of the race rather than of the individual.

C. Nidamental Glands

Eggs destined to leave the body of the female, are provided with some sort of a protective wall or capsule. In water this does not need to be a very complicated structure, but exposure to dry air demands a shell of some kind.

It is apparent that fertilization must occur before the shell is put on to the egg, otherwise the sperm would encounter an insuperable barrier. Consequently *nidamental glands*, which produce the shell, are located in the walls of the oviduct some distance from the ostium abdominale, in order to allow opportunity for egg and sperm to meet before the shell is added. *Albuminous glands*, that furnish the "white of the egg," are located between the ostium abdominale and the nidamental glands, for this additional nutriment must also be applied after fertilization and before the egg is enclosed within a calcareous shell.

Not only does the calcareous shell protect the exposed egg from injury, but, in the case of many birds, blending colors or blotches, which help to camouflage it from searching enemies, are deposited in the substance of the eggshell.

The aquatic egg of the internally fertilized skates and rays, is enclosed in a purselike horny capsule, supplied at each corner

with curling tendrils (Fig. 378), which entangle it among seaweeds, so that the little skate sways and rocks within its curious cradle with comparative security until ready to emerge.

D. Placenta in Mammals

True mammals provide a placenta for the developing young. This is an elaborate compound vascular organ, made up of interdigitating villi from the walls of the uterus and the allantois of the embryo (Fig. 403), which brings the capillaries of the female into intimate approximation with the capillaries of the fetus, thus establishing a nutritive bridge between mother and offspring.

Fig. 403. — Diagram of the embryonic envelopes of a mammal.

There are further embryonic devices in mammals, like the amnion and other fetal envelopes, which provide for the welfare of young reptiles, birds and mammals, and should be remembered in reckoning up the anatomical contrivances that aid in the preservation of the species.

6. Degenerate and Rudimentary Organs

With the downfall of the pronephros and mesonephros and the establishment of the metanephros in amniote vertebrates, there are left behind several structures in the developing animal that are deprived of their original usefulness. As already indicated, some of these structures, like the mesonephric tubules which become transformed into the ductuli efferentes in the epididymis of the male, are rescued and made over to serve a new function. Many other structures, however, find their way to the anatomical rubbish pile, where they remain as useless parts of the animal mechanism, even becoming a source of pathological troubles.

There are also various *rudimentary organs* laid down, that remain useless because they never attain functional efficiency. These are unlike *degenerate structures* in the sense that they are incipient, never having developed, while degenerate organs are those that have had their day.

It is quite important for the pathologist to be grounded in comparative anatomy, because it is just these degenerate anatomical relics and rudimentary structures that are most likely to prove

the focal points for the formation of cysts, tumors, and other bodily abnormalities.

The young embryo presents a condition with respect to the reproductive apparatus that suggests a hermaphrodite with the rudiments of both sexes present. As development proceeds one sex becomes dominant, and the structures which characterize the other sex fade into the background as degenerate or rudimentary remains. There results a homology or equivalence in the anatomical details of the two sexes which is indicated in the following *Table of Homologies*, adapted from Wiedersheim.

TABLE OF HOMOLOGIES OF STRUCTURES DERIVED FROM THE MESONEPHROS AND ITS ASSOCIATED DUCTS

		MALE	FEMALE
Mesonephros	Sexual part	EPIDIDYMIS (in part) Rete testis Ductuli efferentes	Epoöphoron (in part)
	Urinary part	Paradidymis Ductuli aberrantes	Paroöphoron
Wolffian Duct	Proximal part	EPIDIDYMIS (in part) Ductus epididymidis	Epoöphoron (in part) Gærtner's duct
	Distal part	DUCTUS DEFERENS Appendix epididymidis	Weber's organ
Müllerian Duct	Proximal part	Appendix testis	FALLOPIAN TUBES UTERUS
	Distal part	Uterus masculinus Colliculus seminalis	VAGINA Hymen

The organs in the Table of Homologies indicated by capital letters are functional, but the others are degenerate useless structures, or of doubtful function.

The *epoöphoron* of the human female is an organ lying between the layers of the broad ligament of the uterus, composed of eighteen or twenty anastomosing mesonephridia that are closed at both ends. In ruminants, perissodactyls, and pigs, the mesonephridia forming the epoöphoron are connected with a fragment of *Gærtner's duct*, which corresponds to the Wolffian duct in the male.

The *paradidymis* and the *paroöphoron* in the two sexes respectively, are all that remains of the posterior mesonephridia. The paradidymis lies within the spermatic cord near the globus major

of the epididymis, and both the paradidymis and its homolog in the female, the paroöphoron, are found only in older embryos and young children.

The *ductuli aberrantes* are also tubules, originally nephridia, blind at one end and opening into the duct of the epididymis. There may be one, two, or several of them, although the number is usually two. They lie between the testis and the epididymis, and the "inferior ductule," which is the more constant of the two, may attain the length in man of two inches.

The *appendix epididymidis*, (Fig. 381), is probably the degenerate tip of the Wolffian duct, and it lies upon the globus major of the epididymis. Toldt found it present in twenty-nine out of one-hundred and five human autopsies. A similar structure is sometimes found in the female, where it is known as *Weber's organ*.

The *appendix testis* is a small spherical sac (Fig. 381), attached to the testis, representing the tip of the Müllerian duct. It has been reported as present in ninety per cent of the cases examined.

The other end of the embryonic Müllerian duct remains in the male in the form of the *prostatic utricle* or *uterus masculinus*, a small sac homologous with the female vagina. It is embedded in the prostate gland along with the base of the urethra, and is usually distally bifid (Fig. 381), which is additional evidence that it represents the remains of coalescing oviducts.

Around the opening of the uterus masculinus is a small fold of tissue, the *colliculus seminalis*, which marks the end of the Müllerian ducts, and is homologous with the *hymen* of the female, that partially separates the vagina from the vestibule, and likewise locates the true termination of the Müllerian ducts.

7. Apparatus for "Sexual Selection"

There are notable secondary differences between the sexes, particularly among the higher vertebrates, that are neither devices to aid in copulation, nor holdfasts for the prehension of the female by the male, and yet which play a part in the whole scheme of reproduction. These devices are usually peculiar to the male, and in general take the form of ornamentation and coloring, or of organs of offense and defense.

The consideration of these facts led Darwin to formulate his supplementary theory of "Sexual Selection," in order to explain the presence of these modifications in male animals, since the

theory of natural selection seemed inadequate to account for their origin. According to this explanation, organs of offense and defense, such as horns and tusks appearing in males and not in females, were not primarily for warfare with enemies, else the females would be similarly armed, but were developed for battles between males of the same species competing for the possession of the females. Particularly in the case of polygamous males, like seals and ruminants for example, in which there is an obvious rivalry for the females, there is a pronounced development of these secondary sexual organs of offense and defense.

Similarly the distinctive ornamentation and coloration of certain males, particularly among birds, is regarded as having been called forth in the interests of selective mating, the critical females choosing those males which present the most captivating appearance.

Darwin says: "In most cases, the differences of structure between the sexes are more or less directly connected with the propagation of the species."

Instances of male secondary sexual characters that have a racial rather than an individual significance, are the hooked lower jaw of the salmon during the breeding season; the nuptial frill along the back of the male *Triton* (Fig. 29, F); the elaborate vocal apparatus of serenading toads and frogs; the throat pouch of some lizards; the comb, wattles, topknots, plumes, and spurs of birds; the lion's protective mane; and the tusks, horns, and antlers of certain mammals. These peculiarities are absent from the corresponding females.

The distinctive secondary sexual characters of mammals more often take the form of weapons for warfare between the males, while male birds are more given to ornamentation and coloration than females.

It is quite likely that certain endocrine glands, to be considered in the next chapter, are directly responsible for the sexual behavior of animals, and the development of their secondary sexual characters, thus indirectly insuring the life of the species. The greater natural pugnacity of the male, as well as his more vivid coloration and more elaborate ornamentation, may follow as the inevitable physiological consequence of a sexual difference in metabolism, as determined by his peculiar outfit of endocrine glands. This explanation removes some of the responsibility in mating be-

havior from the problematical discriminating judgment of the "weaker sex," and places it upon a surer, less subjective foundation.

Whatever the true explanation, it is apparent that such sex-limited characteristics have somehow been evolved in the interests of the species rather than of the individual, for frequently the possession of excessive ornamentation or of striking colors, renders the individual himself more conspicuous in the presence of enemies.

Finally, sexual selection in man involves much more than physical characters, but there is no doubt that form and feature, even in post-caveman days, play an important rôle, and as such are subsidiary to the reproductive apparatus as a whole.

IV. DETERMINATION AND DIFFERENTIATION OF SEX

The *determination of sex*, as pointed out in Chapter VI, probably occurs at the time of the fertilization of the egg, depending upon the chance combination of the sex chromosomes. The *differentiation of sex*, on the other hand, or the development of visible distinctive sex characters, does not occur in man until about the ninth week of fetal life, although, according to Keith, the testes within the body cavity are distinguishable from the ovaries by the seventh week.

The human external genitalia of the two sexes at first cannot be told apart. At the stage of about the sixth or seventh week, when the legs are still simply two stubs on either side of the embryonic cloaca (Fig. 404), an elevation, the *genital eminence*, tipped by a conical projection, the *genital tubercle*, appears just within the anterior margin of the cloacal opening. Around the genital eminence a pair of folds form. These are the *labio-scrotal folds*, which are destined to become the labia majora of the female and the scrotal sac of the male. Soon the genital tubercle elongates somewhat, and a slit, the *urogenital opening*, develops along its ventral surface. Next the lateral margins of the slit elevate to form a second pair of enclosing folds, the *inner genital folds*, or the future labia minora of the female.

In the male the genital eminence with its projecting tubercle elongates still more into the *corpus spongiosum* and the *glans* of the penis, the urogenital slit, meanwhile, closing over to form the penile part of the urethra. The inner genital folds become the

two *corpora cavernosa* and join together side by side below the corpus spongiosum to complete the body of the penis, while the labio-scrotal folds draw down and grow together to form the scrotal sac. The seamlike ridge, or *raphe*, along the mid-ventral ridge of the scrotum in the adult, represents the line of fusion between these embryonic structures.

In the female the genital eminence and the tubercle remain comparatively undeveloped, in the form of the *clitoris*, while the urogenital slit expands into the vestibular entrance to the vagina, and the two sets of folds on either side shape up into the labia minora and the labia majora. The anterior fusion of the outer labio-scrotal folds which make the labia majora, becomes the *mons Veneris*.

So-called human "hermaphrodites" usually present intermediate embryonic features with respect to the external genitalia, as, for instance, a small undeveloped penis with an unclosed urogenital slit along the ventral side, quite like the cloacal, grooved penis of the turtle. The general relations of the genitalia, both external and internal, of the two sexes in man, are shown in Figs. 405 and 406.

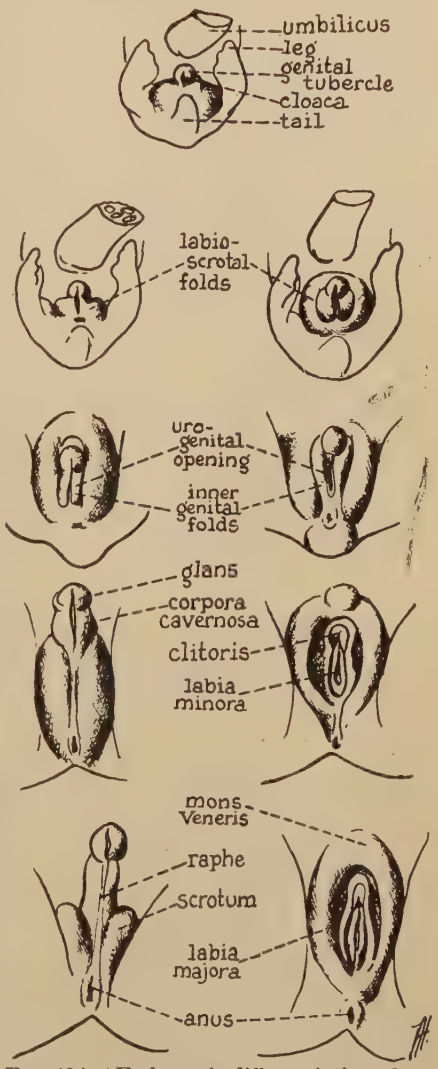


FIG. 404.—Embryonic differentiation of external genitalia. (After Gray.)

V. PERIODICITY IN REPRODUCTION

After sexual maturity is reached, most animals exhibit a periodical recurrence of reproductive activity. This, as applied to the species, may be called the *breeding season*. Within the breeding season itself the individual animal may arise to a single sexual crisis, or may undergo several rhythmic waves of sexual activity, while between breeding seasons the pairing instincts and behavior are in abeyance.

The onset of the breeding season is probably due to a variety of causes, both external and internal, which differ largely in various groups of animals. There is some underlying common ground

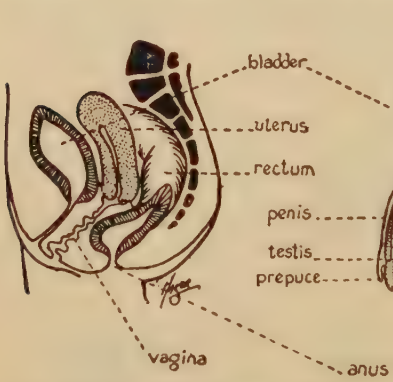


FIG. 405.—Sagittal diagram of female genitalia.

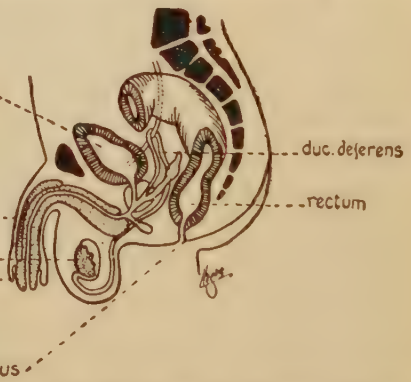


FIG. 406.—Sagittal diagram of male genitalia.

however, for it is apparent that the reproductive cycle of most plants and animals is timed more or less to accord with the changing seasons, and to occur at a time that is favorable for the development of the forthcoming young. This is the spring or early summer in most cases.

There is a curious adaptation between the breeding season of bats and a favorable time of year for the appearance of the future offspring. Pairing is effected in the fall, after which the sexes go their separate ways to different hibernation quarters, males in one place and females in another, where they literally "hang up" for the winter. Since the period of gestation in the bat is only two months, the young would normally be due to appear during the somnolent hibernation period, an impossible state of affairs, were it not for the fact that fertilization is not consummated for several

months after copulation, the sperm remaining viable in the oviducts of the female throughout all that time.

No doubt seasonal temperature is one of the factors that initiates the breeding season of plants and animals. A host of aquatic forms, for example, respond sexually to the rising temperature of the water in the spring of the year. Fishes in schools together shift into warmer shallow or surface waters to spawn, while amphibians and reptiles, arousing from their winter lethargy, proceed at once to boost the census returns in their cold-blooded world. Birds stream north in their great "Canterbury Pilgrimage" as soon as the cold of winter in our northern latitudes has given way to the breath of spring, although it requires some other things than the factor of temperature change to account for the remarkable nuptial flight of their migration. Mammals generally also exhibit enhanced vitality and courtship behavior at this season. Even man, in whom the breeding season has extended to include all the year, feels the spell of spring, so that Tennyson states a biological fact when he sings:

> "In the Spring a livelier iris changes on the burnished dove;
> In the Spring a young man's fancy lightly turns to thoughts of love."

The breeding season of the fishes of the Nile is during the annual period of inundation, and lungfishes (Dipnoi) which pass the dry season burrowed inactively in the mud, breed at once when the rainy season begins again and are thereby restored to activity.

It is rather remarkable that hibernating animals, as well as æstivating lungfishes, proceed immediately to the business of propagating the species when they awake, starved and hungry after their dormant sleep, before they attend to their own individual needs. This is a good illustration of the imperative law of reproduction, which places the preservation of the species above the welfare of the individual.

In the same self-forgetful way the salmon of the Pacific Coast, when they leave the ocean for the long perilous run up rapids, waterfalls, and past countless dangers for many hundred miles to their breeding grounds in the upper reaches of the Columbia and Yukon rivers, ascetically forego all feeding, and devote themselves entirely to the great adventure of reproduction.

It is entirely probable that some internal factor, perhaps a physiological urge set in motion as a consequence of rhythmical met-

abolic processes, must be called upon to account for the astonishing behavior of the salmon. It is certainly not entirely because their gonads have swollen to a degree that demands immediate action, for in the "Silver Horde" of the salmon run are found fishes in all stages of sexual development. Moreover, it has been pointed out by Jacobi that the eel, *Anguilla*, which migrates in the opposite direction from fresh to salt water for its one breeding season in a lifetime, does not exhibit enlarged gonads until it reaches salt water.

The breeding rhythm of some animals is even gauged to a certain time of day. Thus, amphioxus in the Mediterranean region, always spawns at sundown, and the "palolo worm" of the South Pacific, *Eunice viridis*, produces its myriads of eggs and sperm, which color the water for miles about, at daybreak of the particular day falling in the last quarter of the moon in September and in October.

Among mammals during the breeding season, the female passes through an *œstrus cycle*, or "heat," usually following *menstruation*, with which it should not be confused. The œstrus prepares the egg for fertilization, while menstruation prepares the uterine wall for the implantation of the fertilized egg. If only one œstrus is experienced during the breeding season, the animal is said to be *monœstrus*. *Polyœstrus animals*, on the other hand, are those in which recurrent œstrus periods follow each other throughout the breeding season.

In the human female the breeding season is not dependent upon external factors, but extends continuously from the time of puberty until the "menopause" at 45 or 50 years, throughout which time the œstrus, unless interrupted, normally recurs rhythmically every four weeks.

Ethnologists find evidence of a former primitive breeding season in man, in the annual feasts of savages, and the yearly festival of the Saturnalia of classical times, when great sexual license prevailed.

Domestication frequently works changes in the periodicity of reproduction. Many wild animals refuse to breed at all in captivity, while domesticated animals, such as cattle, for example, have been changed from a monœstrus to a polyœstrus condition, and the breeding season itself has been greatly extended, as in poultry, to include practically the entire year.

VI. CARE OF THE YOUNG

The distinctive secondary modifications in the female largely have to do with the care of the young. This function has its beginnings in the unconscious equipment of eggs with nutritive materials, and in the provision by the female of a sheltering uterus or brood sac of some kind. Later in evolution, parental care may take the form of building nests in which to incubate eggs after they have been laid, and in behavior that supplements the helplessness of the newly hatched or born.

In the higher mammals there is a prolonged period of dependence upon the parents after hatching or birth, which makes schooling possible through association with the parents. In this way traditions and acquired wisdom are handed on among animals as soon as an adequate vehicle, by way of brain equipment in the young, is elaborated for it.

The lower animals, on the other hand, never have any schooling. They are supplied once for all with a single "box of tricks," or instincts, and, as soon as they come into the world, they know as much as their parents, or at least are not in the way of profiting by what their parents have gained. Hence, a prolonged dependence upon parental care is the mark of superiority, since it furnishes the soil in which budding intelligence may grow and flourish.

The dominance of mankind is correlated with the fact that the education involved in family life is extended over such a relatively long time. In the case of modern civilized man, in fact, the children do not gain independence of the parents in the most fortunate instances until at least a third of the entire span of life is past.

All transitions are encountered from egg laying without parental incubation (*oviparous habit*), to prolonged gestation within the body of the female, the young being "born alive" (*viviparous habit*). Certain sharks, teleosts, urodeles, lizards, and snakes, are said to be *ovoviviparous*, since there is a close race between hatching and birth, with the two events occurring practically at the same time.

A curious instance of the parental care of the eggs in fishes, is shown by the "silversides," *Menidia notata*, of the Atlantic shore. This little teleost lays its eggs only at the time of the highest tide, when they are buried far up in the wet sand or at

the roots of the shore grasses. As the tide recedes they are left in a safe moist situation out of the reach of aquatic enemies which would devour them. After a period of development, the young fishes kick out of their spherical prisons at some later high tide, and go to sea after the tradition of their kind.

Some of the curious shifts employed by various amphibians in the interests of their eggs and young, have been previously mentioned in Chapter II.

Birds are notoriously nest builders. Such structures are not primarily shelters or refuges for the birds themselves, as much as they are places for incubating the eggs and cradling the young after they are hatched. Even when there is no incubation by the parent, the eggs are usually deposited in some situation favorable to obtaining somehow a sufficient amount of heat to accomplish development. Thus, fishes frequently resort to waters warmer than usual in which to spawn, and turtles deposit their eggs in sand where the heat of the sun has access to them. Sea turtles, whose young are liable to a greater hazard than those of land turtles, come ashore and abandon, upon the friendly doorstep of sand and sun, as many as 150 to 200 eggs. The untaught young upon hatching promptly take to the water, although, as in the case of Darwin's famous Galapagos turtles capable of living for over a century, they know all that it is necessary for a turtle to know on the day they are born, and length of life for them presents only a dreary waste of monotony unrelieved by the stimulating adventures of one capable of traveling far along the highway of experience.

Alligators pile up a swampy nest of rotting vegetation in which to leave their eggs, the fermenting mass engendering the amount of added heat requisite for bringing the eggs to the hatching point.

A few fishes, many lizards and most snakes, are viviparous, but the amount of care bestowed upon the newly born by these animals is practically negligible. With mammals, however, in which postnatal care is obligatory, there is an ever increasing degree of provision for the young, culminating in man.

CHAPTER XVI

INVOLUNTARY REGULATION (GLANDS OF INTERNAL SECRETION)

I. IN GENERAL

There are two general devices, nervous and chemical, for effecting coördination within the animal body. The former is somewhat like a telegraph system, whereby messages are conveyed from one point to another without material transfer, while the latter is more like the parcel post, in that substances produced by certain organs are distributed through the blood system to other parts of the body, where they may bring about results affecting the entire organism.

The chemical regulators of the body have their origin in glands. Some glands, as, for example, those of the digestive tract, are provided with ducts, and furnish chemical substances called *enzymes*, which are indispensable agencies in the utilization of food materials. Others have no ducts and can only deliver their products by means of blood vessels, with which they are in intimate contact. These are the *endocrine glands*, or glands of "internal secretion." The chemical substances which they elaborate from the blood are termed *hormones*, or "exciters," though they may act as restraining bridles as well as stimulating spurs. Hormones, like enzymes, act in very small quantities, which suggests that they may be catalytic in their action, that is, hasten chemical action without themselves undergoing any permanent change, and they may also bring about both developmental and functional results.

The total mass of human endocrine glands all rolled together would form, according to an eminent English biologist, a parcel small enough to "go in a waistcoat pocket," yet their importance is so great that, with the advance of knowledge, gained largely through pathological studies and animal experimentation within the last quarter century, a whole new biological science of *Endocrinology* has arisen, absorbing the attention of a small army

alists and possessing a rapidly increasing literature all

docrine system involves more than the ductless glands since there are several glands having ducts, for example, the liver, pancreas, and gonads, that also liberate hormones directly to the blood, as well as substances through ducts.

There are, moreover, certain substances not produced by glands which act through the blood in a fashion similar to that of hor-

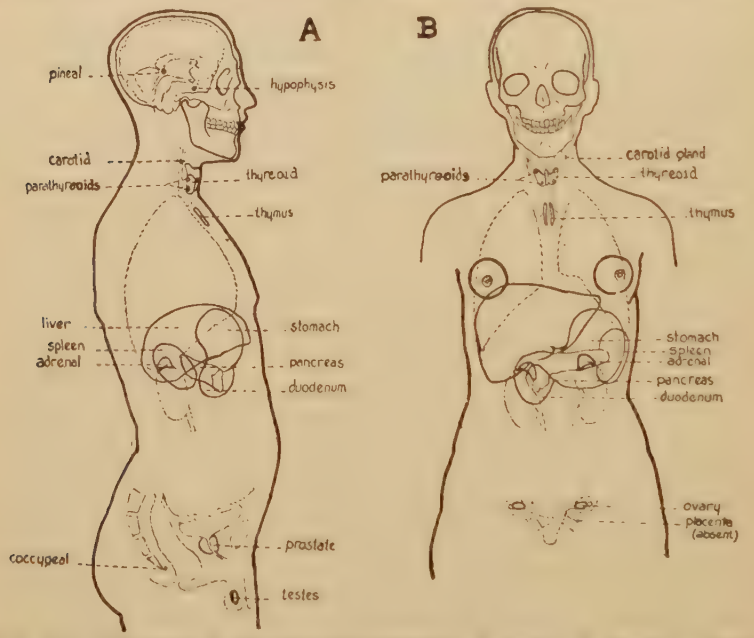


FIG. 407.—Diagram of the endocrine system. *A*, male; *B*, female. (From chart in *Endocrinology and Metabolism*, edited by L. F. Barker. D. Appleton and Co.)

mones, as, for instance, carbon dioxide resulting from the activity of muscle tissues, which is transported through the medium of the blood stream to the respiratory nervous center in the medulla, where the movements essential to breathing are regulated.

The endocrine glands are subject to great variation, and are largely interdependent, rarely acting singly in performing their services to the organism.

The interlocking endocrine system among other things is responsible, in part at least, for (1) the time, order, and rate of

development of organisms; (2) the metamorphosis of amphibians; (3) the adaptive coloration in certain larval salamanders; (4) the development of "secondary sexual characters"; (5) a considerable part of visceral control; and (6) many phases of behavior, particularly the "emotions," which contribute so much to the psychic life and the determination of "personality."

Upsets in the balance of endocrine activities result in various pathological manifestations, while the loss of certain of these glands of internal secretion, results fatally. The possibility of controlling and regulating the functions of the ductless glands, has opened a new field for experimentation and medical practice, with the inevitable and often deplorable accompaniment of much unfounded speculation and quackery.

According to their general location, the principal endocrine structures (Fig. 407), may be grouped into four categories: (1) *pharyngeal* (thyreoid, parathyreoid, and associated glands); (2) *cranial* (pineal, anterior and posterior pituitary); (3) *sexual* (testes, ovaries); and (4) *abdominal* (islands of Langerhans, suprarenals).

No ductless mass of cells which is not muscular, nervous, or skeletal, can escape the suspicion of being involved in the endocrine system.

II. PHARYNGEAL GLANDS

1. Thyreoid

The vertebrate pharynx is a region of much evolutionary modification. One of the oldest structures found there is the *thyreoid gland*, foreshadowed in the *endostyle* of the tunicates and amphioxus (Figs. 10 and 14), where it is an open groove in the floor of the pharynx, lined with mucus-producing cells and supplied with a column of long cilia along its bottom, which by their movement keep the mucus advancing down the gullet in a continuous stream (Fig. 311). Food particles, entangled in this sticky esculator, are thus insured delivery into the digestive tube proper, instead of escaping through the numerous gill slits.

In other vertebrates there is a similar evagination of ectodermal tissue from the pharyngeal wall at the region of the second pair of gill pouches (Fig. 408), which corresponds to the endostyle. It begins to develop very early in man, when the embryo is only about 1½ mm. in length, and does not fail to put in its appear-

every vertebrate. It soon loses connection with the [illegible] however, and becomes a ductless gland, made up of a [illegible] of closed follicles and surrounded by connective tissue. The duct of this embryonic thyreoid gland still remains open during the "Ammocœtes" stage of the lamprey eel, but is obliterated in other vertebrates, and in man disappears by the eighth week of fetal life, although its place of former opening is marked by the *foramen cæcum* at the base of the tongue (Fig. 409).

The thyreoid grows slowly but steadily throughout the prenatal period, until at birth its weight is about 0.125 per cent of the total

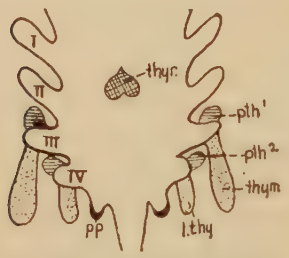


Fig. 408.—Diagram showing the origin of various branchial epithelial structures. *l.thy.*, lateral thyreoids; *pth.*, parathyreoids; *pp.*, post-branchials; *thyr.*, median thyreoid; *thym.*, thymus; *I–IV*, branchial pouches. (After Kohn.)

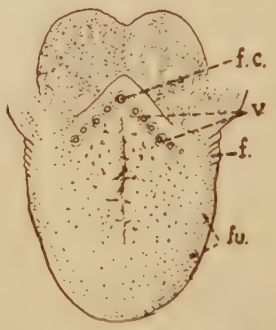


Fig. 409.—Dorsal view of the human tongue. *f*, foliate papillæ; *f.c.*, foramen cæcum; *fu.*, fungiform papillæ; *v*, vallate papillæ. (After Parker.)

weight of the body. After birth, while its actual weight still increases, its relative weight decreases, so that eventually in adult life it normally has a weight of about 40 grams, being somewhat heavier in the human female than in the male. According to Hatai and Johnson there is no difference in the weight of the thyreoid gland of the two sexes in rats.

The blood supply of this gland, which comes from the subclavian arteries, is very generous. Wiedersheim states that it may equal or even exceed that of the brain.

In fishes the thyreoid gland is composed of several groups of loose follicles, scattered along the ventral aorta, but in amphibians, reptiles, and birds it becomes increasingly compact, and in mammals finally comes to assume a bilobed shape, with flattened *lateral portions* joined together by a connecting *median isthmus*

(Fig. 410). The right lobe is frequently somewhat larger than the left lobe.

The shifting of the thyreoid gland from its anterior embryonic position in the floor of the mouth to a posterior situation near the upper part of the trachea, is made possible because it is in no way anchored or hampered at its point of origin by a duct. Every time the act of swallowing takes place, in fact, it moves up and down with the larynx.

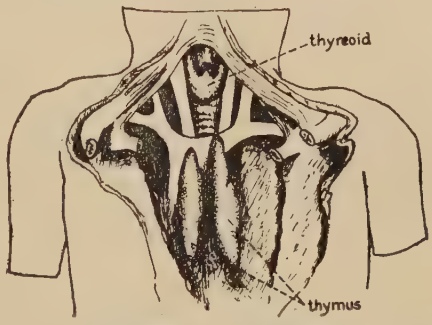


FIG. 410.—Thyreoid and thymus in a child one month old. (After Olivier.)

There has been obvious phylogenetic change in function in this organ. From a device useful for the mechanical manipulation of food particles taken in with water, it has become an endocrine structure, producing a hormone affecting the oxidation processes, and consequently the rate of living. It has been aptly called the "pace-setter," or metabolic regulator of the body.

The substance produced by the thyreoid gland is *thyroxin*, a compound rich in iodine, which has not only been chemically isolated and crystallized, but also artificially synthesized. When introduced into an animal, either with food, or by subcutaneous or intravenous injection, it may produce marked results. Tadpoles, for example, fed with thyreoid gland, change into tiny frogs without "growing up," and when thyreoidectomized they grow up into large tadpoles without metamorphosis.

Human beings with deficient thyreoid apparatus may develop into unfortunate defectives, called *cretins*, having retarded or imperfect mental and physical development; or they may suffer from *myxodema*, a disease characterized by an overgrowth of connective tissue or fat, loss of hair, weak muscular development, œdematous skin, impoverished blood, deficient sexuality, lowered metabolism, nervous depression, and frequently impaired mentality. This condition may be relieved or removed entirely, when taken in time, by the proper administration of thyreoid extract.

An excessive development of the thyreoid gland results in abnormally increased oxidation, and manifestations of disease such

as *exophthalmic goitre*, in which the patient becomes extremely nervous and thin, exhibiting characteristically protruding eyeballs. This is a serious progressive disturbance not to be confused with *common goitre*, which is caused by thyreoid deficiency and is more amenable to treatment. Common goitre usually results from living in a region where the soil, and consequently the food materials derived therefrom, lacks iodine, which is an essential constituent of thyroxin.

2. Parathyreoids

Budding off embryonically from the walls of the gill pouches are various epithelial structures that later become glandular. Among these are the epithelial bodies, parathyreoids, postbranchial bodies, and thymus glands.

In cyclostomes, for instance, there are seven separate pairs of these structures which form the *epithelial bodies*, situated in the *ventral* region of the gill pouches. In teleost fishes they are lacking, but from the Amphibia on, there are usually present at least two pairs of glandular structures that are probably homologous with epithelial bodies, since they arise like them from the ventral region of the gill pouches, particularly from the third and fourth pairs. These bodies, which have been identified in lizards, some birds, and many mammals, are known as *parathyreoids* (Fig. 408), because they eventually assume a position either in direct contact with, or close to, the thyreoid gland. In man they are small yellow encapsuled bodies, one pair of which comes to lie embedded in the median dorsal surface of the thyreoid gland on either side, while another pair is just above the thyreoid, and still others may be distributed farther down the sides of the neck.

Although in man their weight altogether is only about fifty centigrams, and their size but a few millimeters in diameter, they are indispensable to life, as their complete removal always results in death. Children's convulsions are found to be correlated with parathyreoid deficiency, and the fatal tetanic fits, which almost invariably followed thyreoidectomy in the earlier days, are now known to be due, not to the removal of the thyreoid gland in itself, but to the accidental extirpation of the parathyreoids during thyreoid operations.

It is apparent that the hormones produced by the parathyreoid glands play an important rôle in the calcium metabolism of the body.

3. Thymus

The *thymus glands*, like the parathyreoids, have a multiple origin, but they come from the *dorsal* region of the gill pouches instead of the ventral region (Fig. 408). Although present in all vertebrates, in some fishes they remain epithelial in character, while in higher forms they become lymphoid and are highly vascular. The different embryonic elements of the thymus frequently fuse together to form masses of tissue down either side of the neck (Fig. 410).

In mammals, including man, the thymus gland is principally derived from the posterior epithelium of the third gill pouch. It reaches its actual maximum in size at about the time of puberty, although its greatest relative size is attained much earlier, in infancy.

The total removal of the thymus is not fatal, but its function is not known, although Gudernatsch has shown that in tadpoles fed upon thymus, growth is accelerated and metamorphosis is delayed, an effect just opposite to that obtained when thyreoid is employed as food.

Recent researches have by no means sustained the hypothesis that the thymus is an endocrine gland. Hoskins summarized the present state of our knowledge by saying: "In all probability the organ is of significance in the physiological and pathological processes, merely by virtue of its lymphoid character."

4. Postbranchials

The postbranchials (Fig. 408) as their name indicates, are the most posterior of the series of pharyngeal derivatives, which

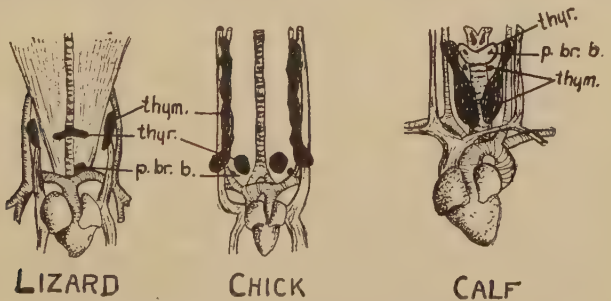


FIG. 411.—Pharyngeal glands. *thym.*, thymus; *thyr.*, thyreoid; *p.br.b.*, postbranchial bodies. (After DeMeuron.)

may be suspected of endocrine activities. They arise behind the fifth pair of gill pouches. Only the left postbranchial body

develops in lizards (Fig. 411) and their occurrence in birds and mammals is doubtful. The postbranchial bodies in function are probably not connected with any particular internal secretion, but they have a mission in common with other lymphoid structures throughout the body, like the *tonsils*, which are also pharyngeal derivatives.

III. CRANIAL GLANDS

The hypophysis and pineal bodies are two structures on the ventral and dorsal sides of the brain respectively, which require special consideration in this connection.

1. Hypophysis

The hypophysis is a compound structure of double origin, located most inaccessibly just behind the optic chiasma in the space between the roof of the mouth and the ventral side of the brain. In man and the higher vertebrates it lies ensconced in the *sella turcica*, which is a space hollowed out in the sphenoid bone of the cranial floor.

Phylogenetically it is very old, being universally represented in all vertebrates, and osteological evidence has been presented (Moody) that it was well developed even in the ancient dinosaurs.

Its relative size decreases from the lower to the higher vertebrates. In adult man it is about "as large as a hazel nut," or rather less than a cubic centimeter in bulk, weighing normally about 0.5 grams.

In myxinoids it discharges its secretions directly into the pharynx, but otherwise throughout vertebrates it has become a ductless gland, concerned solely with internal secretion.

The name pituitary body, meaning "phlegm," was given to this structure, because Galen and the early anatomists, who had already discovered it, thought that it produced nasal secretions.

The pituitary body consists of three parts, one posterior, one intermediate, and one anterior in position. The *posterior lobe* in the adult mammal consists of a neural portion derived from the brain (*pars neuralis*, formed from the infundibulum, infundibular process, etc., Fig. 412). This neural portion consists of a lining of ependymal cells and a mass of neuroglia cells and fibers. There is no histological evidence that the *pars neuralis* is secretory.

The *pars intermedia*, which in most mammals is wrapped around the *pars neuralis*, is epithelioid and apparently secretory. Both the *anterior lobe* and the *pars intermedia* have a common embryonic origin from an ectodermal invagination, *Rathke's pouch*, from which they are eventually cut off. Cushing compares the whole pituitary apparatus to a ball held in a boxing glove, in which the ball represents the posterior lobe, the cover of the ball the *pars intermedia*, and the boxing glove the enveloping anterior lobe.

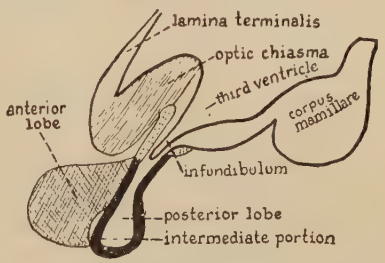


FIG. 412.—Diagram showing the relationships of the hypophysis in the adult brain. The infundibular portion of the hypophysis is represented in black; the tuberal portion is stippled; and the anterior lobe is cross hatched. (From McMurrich, after Tilney.)

The anterior lobe is made up of at least three kinds of cells that stain differently and consequently are of diverse chemical nature. On the periphery are *basophil* cells, which take basic stains readily, in the center are *acidophil* cells, amenable to acid stains, while *chromophobe* cells that are not easily affected by either basic or acid stains, are scattered throughout the structure. The chromophil cells, both acid and basic, increase with the evolution of the vertebrate series.

The function of the anterior lobe of the hypophysis is not the same as that of the posterior lobe. It has to do with growth. Giantism, dwarfism, and acromegaly, or excessive growth of certain bones and joints, are all apparently correlated with abnormal conditions of the anterior lobe.

The hormones produced by the posterior lobe of the pituitary have to do with fat formation, the production of urine, and the development of the sexual apparatus, the whole structure in the female increasing in size during pregnancy. It also affects the involuntary muscles, particularly in the walls of the blood vessels and so tends to modify blood pressure. An extract of the posterior lobe, *pituitrin*, is known to increase the blood pressure by stimulating the smooth muscle cells to contraction and thereby diminishing the caliber of the arterioles. It is used to some extent in obstetrics to accelerate the contraction of the uterus and thereby hasten the delivery of the child; or when adminis-

tered in a later stage of labor it assists the uterus to return to its resting condition. Riddle, by administering pituitrin to pigeons, succeeded in bringing about a sort of abortion, that is, caused them to lay eggs at an exceptionally early stage of development.

The complete removal of the hypophysis probably results in death, although the difficulty of access to it, and the resultant unavoidable injury to neighboring brain tissues, may be the reason for fatal results usual in operations upon it.

2. Pineal Body

On the dorsal side of the brain, and completely concealed in higher vertebrates by the dominating growth of other parts, is a small, stalklike evagination of the brain wall, called the *epiphysis*, or *pineal body*. In fact one or another of three different structures, the epiphysis, paraphysis, and the parietal or parapineal organ (Fig. 413), all of neural origin and easily confused as to their probable homologies, are located in this part of the brain.

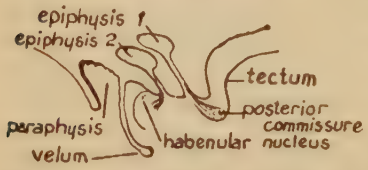


FIG. 413.—A sketch showing in median sagittal section the typical relationships of the paraphysis, and two epiphyses of the vertebrate brain. *1*, *2*, epiphyses. (After Johnston.)

The most anterior of these structures is the *paraphysis*, which lies directly in front of the *velum transversum* at the junction between the cerebral hemispheres and the diencephalon.

The *parietal organ* is sensory rather than glandular, and in certain lizards, like *Sphenodon*, where it reaches its best development, it becomes a median eye of more or less efficiency, reaching the top of the head through a window-like foramen that pierces the skull.

The epiphysis and parietal body, although arranged in tandem fashion whenever both are present, as in cyclostomes, were probably once paired structures lying side by side. The epiphysis is the more constant of the two structures, being almost universally present in vertebrates. Originally a sense organ probably, it has become glandular and even fibrous in character.

The *pineal body* in mammals is the persisting proximal portion of the epiphysis. Its shape resembles that of a pine cone, from which circumstance its name is derived. It is relatively

larger in children than in adults, attaining its best development at about seven years of age, when involutionary changes begin to appear. In man it measures only about twelve by eight by four millimeters.

The pineal body has been known to anatomists since early times, and has always been a source of much curiosity and speculation. Repeated attempts have been made experimentally to discover its activity, and to ascertain significant structural modifications associated with abnormal conditions in the development of this organ, but the results have been conflicting and disappointing.

The fact that it is a highly vascular structure, frequently lobulated like a gland and containing secreted pigment, has raised the suspicion that it may have some endocrine function, but its extirpation does not seem to be followed by unmistakable physiological consequences. While it is, no doubt, a degenerate structure, it may possibly be of physiological importance with some obscure endocrine function, yet hardly more has been proved with regard to it today, than when Descartes (1596–1650) three centuries ago, guessed that it was "the seat of the soul."

IV. SEXUAL GLANDS

As already pointed out in the preceding chapter, the gonads, or primary reproductive organs, not only furnish either sperm cells or eggs, but they are also glands of internal secretion.

Whenever castration occurs before puberty the so-called secondary sexual characters fail to develop. It has been shown that this result is due not to that part of the testis or ovary which produces sperm cells or eggs, but to certain interstitial or glandular cells of endocrine function, which have been called "puberty glands" by Steinach.

1. Male Gonads

There are three kinds of epithelial cells in the testis, namely, spermatogenic, Sertoli cells, and interstitial cells (Fig. 383). The first two make up the seminiferous tubules, while the interstitial cells are grouped around the blood vessels in the spaces between the tubules. They form before the germ cells, and respond differently to various stains, thus indicating their specific character. Moreover, they do not succumb to the lethal effects of the X-ray as quickly as sperm cells.

When an animal is deprived of the hormones produced by the interstitial tissues of the testis there is a tendency for distinctly male characteristics, such as the horns of the stag, the colors of the plumage of male birds, the distribution of hair that marks the male mammal, and peculiarly male behavior in courtship and mating, to revert to a neutral condition.

Interstitial glandular tissue is not found, however, in the testes of all vertebrates, and it is equally true that many vertebrates are without secondary sexual characters.

2. Female Gonads

Small groups of interstitial cells were discovered in the ovary by Pflüger as early as 1863, but subsequent study thus far only goes to prove that they lack the morphological individuality of the interstitial testicular cells, and may not belong to the same endocrine category.

There is, however, in the ovaries of certain mammals, including man, an endocrine tissue, the *corpus luteum*, probably formed from the Graafian follicle after the liberation of the egg, by proliferation of the *zona granulosa* cells, which is unmistakably associated with menstruation, pregnancy, and the production of milk. The exact origin of the corpus luteum, however, is still a matter of controversy. Pearl and Boring have also demonstrated the presence of *lutein cells* in the ovary of the hen, although the mammalian functions just enumerated do not occur in birds.

It will be noted that according to the theory of "sexual selection," whatever endocrine tissues are present in either the ovary or the testes, serve the same general purpose of maintenance of the species as do the primary sexual cells produced by the gonads, since secondary sexual characters contribute to the general function of mating and reproduction.

V. ABDOMINAL GLANDS

1. Suprarenals

In man there are two small but important structures, the *suprarenal glands*, weighing only eight or nine grams each, which fit like caps over the antero-mesial ends of the kidneys (Fig. 414). They are enclosed in delicate but firm capsules of connective tissue which separate them from the kidneys to which they are closely adherent. They are relatively the most vascularized organs

of the body, since five or six times their own weight of blood passes through them per minute. They are somewhat smaller in the female than in the male, and frequently in the same individual the one on the right is smaller than that on the left.

Although discovered long ago by Eustachius, who has so many other anatomical discoveries to his credit, their significance and importance as endocrine glands has only recently been made clear by Cannon. The first hormone to be isolated in pure form, *adrenalin* or *epinephrin*, was obtained from these glands. This substance, which has also been chemically synthesized by Aldrich and Takamine independently, is known to chemists as *ortho-dioxy-pheny-lethanol-methylamine*.

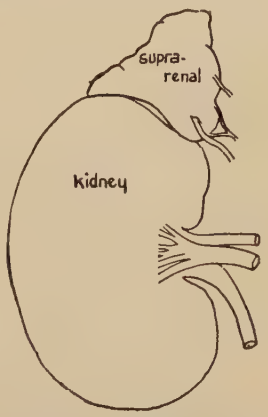


FIG. 414.—Human suprarenals. (After Heitzmann.)

In structure the suprarenals are compound organs, consisting of an outer *cortex* and an inner *medulla*. These two parts are not only morphologically and embryologically distinct, but are also chemically and physiologically different.

In origin there is a close relationship between the medullary cells of the suprarenal glands, which produce the adrenalin hormone, and the sympathetic nervous apparatus. When migrating cells of the central nervous system become detached during development for the establishment of the sympathetic ganglia, they are double in character, although indistinguishable, without recourse to differential staining.

Some of them (*sympathoblasts*) become involuntary neurones of the sympathetic ganglia, while others (*chromoffinoblasts*), although of common origin with the sympathoblasts, are transformed into so-called *chromaffine cells*, since they show a special affinity for chromic acid salts, taking on a brownish color in the presence of the latter. These cells form glandular endocrine masses, and the extent to which they may be stained by chromium compounds is proportional to the amount of adrenalin which they are producing at the time.

It is the chromaffine derivatives of the cœliac plexus in the sympathetic nervous system, which give rise to the medulla of the suprarenal glands. Chromaffine tissue, however, is not confined

to the suprarenals, but may be associated with any of the sympathetic plexuses or ganglia, forming *paraganglia*, or *chromophil bodies* of various sorts. These are frequently associated with blood vessels, as, for example, the *carotid gland*, at the junction of the internal and external carotid arteries, and the *aortic bodies of Zuckerkandl*, two or three in number, which are near the aorta in the human fetus and during early childhood.

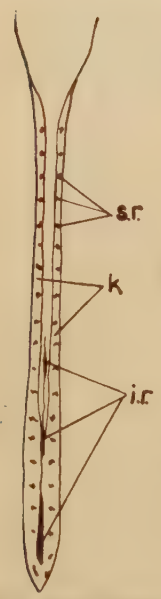


FIG. 415.—Urinary apparatus of an elasmobranch. *k*, kidneys; *i.r.*, interrenals; *s.r.*, suprarenals. (From Wiedersheim, after Grynfeldt.)

In fishes the chrome-staining, adrenalin-secreting tissue is not concentrated into a medulla within a cortex, but is a diffuse double row of groups of cells associated with the trunk-line chains of sympathetic ganglia. During the phylogenetic ascent of the vertebrate series, the neuronic elements of this partnership increase in number and importance, while the chromaffine cells diminish.

In addition to the chromaffine bodies in fishes there are, lying between the kidneys, two elongated masses of tissue, derived from the cœlomic epithelium, named from their position, the *interrenals* (Fig. 415). These are destined to form the *cortical* part of the future suprarenals.

A transitional evolutionary stage is presented by amphibians, in that the original close connection between the chromaffine cells and the sympathetic ganglia is partially lost, and the interrenal tissue comes into close contact with, and begins to envelop, the chromaffine bodies. This new association becomes still more intimate in reptiles and birds, but it is only in mammals that a definite chromaffine medulla becomes established inside an interrenal cortex. The lower the species within the mammalian line, the greater is the relative amount of the cortical component.

It is not yet clear just what the function of the suprarenal cortex is, but its derivation and structure indicate plainly a use entirely distinct from that of the hormones produced by the medulla. According to Swingle the suprarenal cortex has to do with keeping up the acid-base equilibrium of the body by supplying

a hormone which maintains the acid-eliminating function of the kidneys.

The suprarenals undergo precocious growth, reaching their largest relative size in man at about the third fetal month, when they are as large as the neighboring kidneys.

There are various theories as to the function of the chromaffine system. It is known that when adrenalin is injected into an animal there is a decided but comparatively brief rise in blood pressure; the heart beat is steadied, becoming slower and more powerful; there is a quick increase of emergency sugar fuel (glycogen) poured into the blood; and the muscles, particularly the involuntary muscles that are supplied by sympathetic nerves, are thrown at once into their most efficient condition of tonus. Thus, in emergencies, the temporary "strength of desperation" is furnished by the adrenalin, and fatigue is for the time banished.

Although minute quantities of this hormone are essential to the normal processes of metabolism, it is not supplied continuously to the blood in any great quantity, but only as occasion demands, to meet some transient physiological crisis.

At least one pathological condition (*Addison's disease*) is known to be definitely correlated with either deficiency or lesions of the suprarenals. This disease, which was first described nearly a century ago by Addison from Guy's Hospital in London, is characterized on the part of the patient by muscular weakness, low blood pressure, digestive disturbance, and the appearance of peculiar bronze patches upon the skin. Although the course of the disease may be somewhat modified by the administration of adrenalin, a fatal termination seems to be inevitable.

2. The Islands of Langerhans

The *pancreas* is another gland compounded of two kinds of tissues. The pancreatic cells proper are grouped about a drainage system of ducts, and the substances elaborated by them are important digestive enzymes (Chapter XI), which escape through these ducts into the small intestine. Throughout the vertebrates there appear in isolated groups between the cells of this glandular system, distinct interalveolar cells, arranged as anastomosing cords of cells alternating with sinusoids, and forming rounded masses (Fig. 260), which have no outlet by ducts for the substances that they produce, and which, consequently, resort to the endocrine

method of disposal through the blood system. Such interstitial masses of endocrine tissue are known as the *Islands of Langerhans*. It has been ascertained that the hormone which they produce affects carbohydrate metabolism by regulating the use of sugar within the body. Disturbances in this function lead to the pancreatic disease of *diabetes*, which is characterized by an excess of unoxidized sugar in the blood and urine.

In fishes the Islands of Langerhans are condensed into large superficial lumps that may be easily severed from the remaining pancreatic tissue, but in higher forms the characteristic grouping into small isolated masses occurs. It is estimated that in the pancreas of the guinea pig there may be as many as 25,000 "islands." They are rather more abundant in young animals than later in life, and in man make their appearance first in embryos of about 54 mm. in length.

The hormonic principle of this endocrinic tissue has been successfully isolated by Banting and McLeod, who have given it the appropriate name of *insulin*. This hormone is being effectively utilized in the alleviation of diabetes.

3. Spleen

The *spleen* (Fig. 252), for some time suspected of endocrine affiliations, is the largest lymphatic organ of the body. If it is a gland of internal secretion, the hormones which it produces are not essential to life, since its complete extirpation is followed by no results that can be definitely ascribed to it.

Its function is probably similar to that of other lymphatic tissues which have to do with the formation of lymphocytes and the destruction of erythrocytes.

PART THREE

THE MECHANISM OF MOTION AND SENSATION

CHAPTER XVII

SUPPORT, PROTECTION, AND LEVERAGE (SKELETON)

I. THE RÔLE OF THE SKELETON

The vertebrate skeleton is considerably more than a scaffolding for the proper support of the softer parts of the body. There are at least five specific uses to which it is put, namely: (1) giving protection to other parts; (2) making a support for the body; (3) furnishing a firm adequate surface for the attachment of muscles; (4) providing leverage for locomotion; and (5) keeping up a continuous manufacture of blood cells.

The *protective use* is one of the earliest functions of the skeleton to be developed, reaching its greatest elaboration in the armor-like exoskeleton of the arthropods. In vertebrates the protective function is shown by the brain case or skull; the neural arch of the spinal column, enclosing the nerve cord; and the thoracic basket, composed of vertebræ, ribs and breastbone, which provides sanctuary for various important soft organs.

The *skeleton as a support*, that is, as an internal living scaffolding on the outside of which other organs of the body are carried, instead of a dead exoskeleton enclosing the body as elaborated in many invertebrates, is a brand new idea in the animal kingdom, of far-reaching evolutionary significance, and is peculiar to vertebrates. The vertebrate skeleton avoids the limitations to size set by a non-living exoskeleton, since an endoskeleton is a changeable, living structure, which, through its possibility of continuous adaptation, keeps pace with the increasing demands of an enlarging organism. In the "Golden Age" of reptiles, Nature revelled in the possibilities of a living inside skeleton. Dinosaurs, plesiosaurs, iguanodons, theromorphs, with all their monstrous and bizarre kith and kin,

long since vanished, literally lifted tons of flesh into the air upon majestic bony scaffoldings. There still remain elephants on land and whales in water as examples of how far it is possible to go in the matter of size when an adequate internal support is provided.

Since sufficient solid surface must be conveniently placed to give *foothold to the muscles*, the skeleton meets this necessity. It is true that there are various muscles, such as those in the walls of the intestine responsible for peristaltic movement, as well as the sphincters that close the anus or pucker the whistling lips, which are not directly attached to hard skeletal parts, but most muscles are so connected both at their origin and their insertion. The skeleton of flying birds furnishes an excellent illustration of what is meant by having a relatively large skeletal expanse for muscle attachment. In spite of the necessity of economizing weight and gaining compactness in any flying machine, it will be seen that in the bird (Fig. 416), a relatively enormous breastbone, with a thin "keel" at right angles to it, practically doubles the expansive surface for the attachment of flying muscles without adding much to the total weight. The ribs of the bird, too, are much flattened to make the same amount of bone furnish an increased surface, while the ends of the long bones of the leg have a larger relative expanse than corresponding mammalian bones. In man conspicuous skeletal surfaces are found on the innominate bones of the pelvis, which have to do with upright posture, and on the broad shoulder blades, that furnish anchorage for the muscles operating the arms.

Fig. 416.—Skeleton of a bird, showing large surfaces for muscle attachment. (After Bradley.)

In the evolution of higher forms, as soon as water is abandoned for water and air, *levers* appear in the form of legs and wings for purposes of locomotion. Such specialized levers are hardly necessary for a fish, which moves about in a medium sufficiently resistant

to make lateral tail strokes effective. The difference in density between water and air is so great, however, that a mechanism which is successful in water would prove entirely ineffective when operated in the thin and comparatively non-resistant medium of air. One of the first stages in the evolution of locomotion upon land, therefore, has been the elevation of the elongated body from the ground by means of legs so that the amount of frictional surface is minimized, while at the same time the legs become a system of skeletal levers upon which the muscles of locomotion may act in propelling the animal forward. In birds the body becomes poised upon the hind legs alone, a device that accomplishes locomotion as long as contact with the ground is maintained. The front legs meanwhile, emancipated from terrestrial contact, become wings, or levers adapted for flight in air.

The last of the five general uses of the skeleton, that of the *manufacture of blood*, is accomplished by marrow tissue within the hollow bones. Marrow cavities are present in the mammalian sternum, ribs, and cranial bones, but are more pronounced in the long bones of the appendicular skeleton.

Four general kinds of skeletal tissues may be recognized in vertebrates, namely, connective, notochordal, cartilaginous, and bony. These tissues have been briefly described in Chapter VII.

II. THE MAIN SKELETAL AXIS

Vertebrates are bilaterally symmetrical, with the long dimension of the body stiffened by a *skeletal axis*, usually in the form of a backbone, lying between two tubes that similarly run lengthwise the body. The *digestive tube*, which lies below the axis, is ordinarily much longer than the body itself, and consequently is more or less coiled. The *neural tube*, which lies above the axis, is relatively short and straight. It is enclosed at either end and expanded anteriorly into a brain (Fig. 5). The whole apparatus lies along and above its skeletal support and, with few exceptions, is encased protectively by it. Thus the skeletal axis, which is made up of the backbone and skull, is seen to hold intimate and fundamental relations with both the nervous and digestive systems, having evolved primarily to meet the mechanical necessities arising from a locomotor bilateral type of symmetry.

1. Vertebræ

The skeletal axis is for the most part composed of separate bony elements, or *vertebræ*, which lend to the entire structure a certain degree of flexibility without sacrificing the stiffening quality for which the "backbone" stands.

The parts of a typical vertebra are the centrum, neural arch, processes, and foramina, as shown in Figs. 417 and 418.

The *centrum* is the body of the vertebra, on the dorsal side of which is saddled the *neural arch*, a composite structure made up of two *pedicels*, or columns, that merge into two flattened *lamellæ*, which like the sides of a roof, meet at the ridgepole to form the *neural spine*. Through this well protected bony arch the delicate nerve cord safely extends.

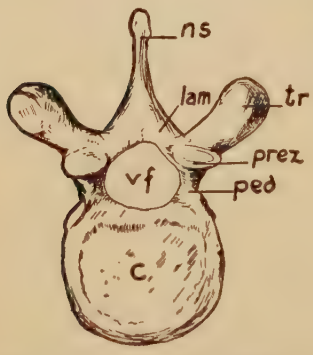


Fig. 417.—The tenth thoracic vertebra as seen from above. *c*, centrum; *lam*, lamella; *ns*, neural spine; *ped*, pedicel; *prez*, prezygapophysis; *tr*, transverse process; *v.f*, vertebral foramen. (From Spalteholz.)

Fig. 418.—The tenth thoracic vertebra as seen from the right. *c*, centrum; *ns*, neural spine; *prez*, prezygapophysis; *postz*, postzygapophysis; *tr*, transverse process. (After Spalteholz.)

In many vertebrates with well defined tails, a second arch, upside down, known as the *hæmal arch*, is present on the opposite or ventral side of the centrum, affording a protected passage-way for the large blood vessels that supply the tail region (Fig. 419).

Extending in various directions from the neural arch are several outgrowths, or *processes*, which offer convenient surfaces either for muscle attachment or for frictional contact of one vertebra upon another. Of these processes the neural spine, already mentioned, forms the keystone of the arch, while two others, the *transverse processes*, which are located at the junction of the pedicel and the lamella on either side respectively,

project laterally somewhat like the exaggerated eaves of a Chinese pagoda.

On the sides of the pedicels are four more processes bearing articular surfaces. The two anterior of these, *prezygapophyses*, are on either side, face upwards, and the two posterior ones, *postzygapophyses*, face downwards. The articular surfaces of the prezygapophyses of any given vertebra rest upon the corresponding articular surfaces of the postzygapophyses of the vertebra next in front after the fashion of a chain gang thus making possible a certain amount of movement between the vertebræ (Fig. 420). The relation of the articular surfaces of the zygapophyses is "onward and upward," that is, the "onward," or anterior end, faces "upward."

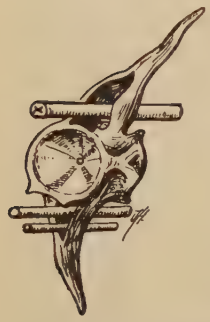


Fig. 419.—A caudal vertebra of a fish, showing hæmal arch, with caudal artery and vein passing through it, and neural arch with nerve cord. (After Jammes.)

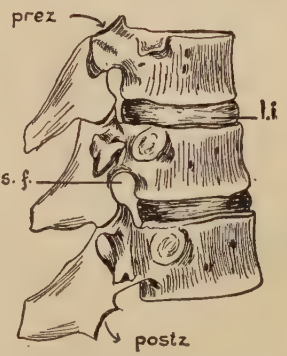


Fig. 420.—The tenth, eleventh, and twelfth thoracic vertebræ, taken from the right to show their articulation by means of zygapophyses. *s.f.*, spinal foramen; *l.i.*, *ligamenta intervertebralia; prez*, prezygapophysis; *postz*, postzygapophysis. (After Spaltenholz.)

Movement of skeletal parts, it should be remembered, depends upon muscles and joints. In those regions of the backbone, therefore, where movement is most needed, as, for instance, in the neck, the various processes of the vertebræ are most elaborated. On the other hand, where rigidity and the absence of movement are desirable, as, for example, in the sacral region, all processes are much reduced.

Foramina, or passage-ways, also are present in the vertebral column, notably the large *neural foramen* formed by the neural arch upon the centrum, in which the nerve cord lies, and the *spinal foramina* (Fig. 420), between the vertebræ themselves, through which the trunks of the spinal nerves, as well as certain blood vessels, find egress.

Finally, all the parts which constitute a typical vertebra un-

dergo the widest variation not only in different species of vertebrates, but even in the different vertebræ making up the backbone of any individual.

2. The Evolution of Vertebræ

A. The Notochord and Its Sheaths

The formation of the vertebræ in the embryo is preceded in every backboned animal, by a temporary skeletal axis called the *notochord*. The position of this temporary axis, which lies lengthwise between the neural cord and the digestive tube, is the same as that of the succeeding vertebral column. In fact the notochord takes part in the actual formation of the vertebral column.

Unlike ordinary skeletal tissue in which intercellular material is excessively developed, the notochordal cells are relatively large at first, with thin walls. They are enclosed in a tough sheath of connective tissue. As the notochord grows older, the cells within the sheath change. Those next the sheath itself form a definite layer of *peripheral notochordal cells* (Fig. 421) while those in the center tend to become vacuolated, losing their outlines and fusing together. The peripheral cells then become transformed into a *secondary sheath* inside the primary one (Fig. 2), with the result that the notochord, as a whole, at this stage might be described as a rigid cylinder made up of the remains of closely packed cells, surrounded by a double sheath and tapering at either end.

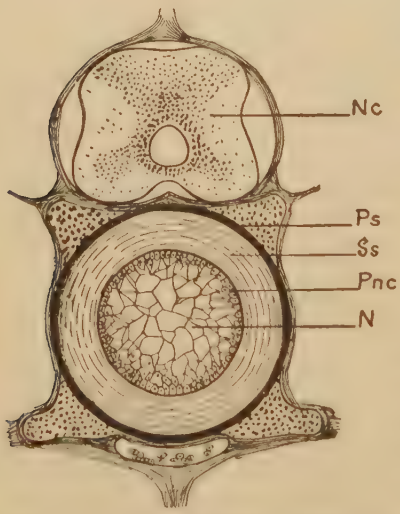


Fig. 421. — Cross section through the notochord and its sheaths, taken from a young dogfish. *Nc*, nerve cord; *Ps*, primary sheath; *Ss*, secondary sheath; *Pnc*, peripheral notochordal cells; *N*, notochord. (Drawn by K. L. Burdon.)

Throughout life in amphioxus and cyclostomes, the vertebral column evolves no further than the notochordal stage, but in other vertebrates, after the notochordal stage is passed, an axial skeleton of another and more complicated kind is attained.

The notochord is, therefore, the oldest part of the vertebrate skeleton, antedating all other skeletal tissues not only during the development of the individual but also in the long phylogeny of the vertebrate type.

B. Formation of the Neural Arch

Although *support* in the form of a stiff rod through the long dimension of a bilaterally symmetrical animal is the earliest function that any skeletal tissue in a vertebrate performs, the function of *protection*, particularly of the precious nerve cord lying just above the notochord, begins to appear very soon after. Along the notochord and on either side of the nerve cord of the lamprey eel, pairs of small cartilage plates arrange themselves, which distinctly foreshadow the future neural arches of the higher vertebrate type, although they may not meet in a "keystone" above (Fig. 422). In later evolutionary stages most fishes, as well as other vertebrates excepting cyclostomes, exhibit these plates joined together into a complete neural arch. The original separateness of the arch from the centrum is clearly established not only by the evidence of embryology, but also by that of comparative anatomy, since distinct sutures between arch and centrum appear in young mammals, as well as in adult alligators and turtles.

Fig. 422.—Diagram of a piece of the notochord of a lamprey eel, with cartilaginous arches, indicating the beginnings of vertebræ, saddled upon it. The arrow shows the position of the nerve cord.

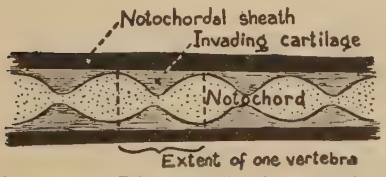


Fig. 423.—Diagram of a long section through a developing backbone at the stage when the notochord is being invaded by rings of cartilage to form the centra of the vertebræ.

C. Formation of the Centra

Soon after the arches start to form around the nerve cord, the notochord begins to be superseded by the centra of the future vertebræ. Opposite the paired cartilaginous plates that are forming the neural arches, rings of cartilage appear around the notochord just outside the notochordal sheaths, each one of which is destined to form the centrum of a future vertebra. As these cartilage rings grow faster on the inside than on the outside, they gradually invade the notochord by pinching into

its cylindrical mass. Figure 423 shows diagrammatically a long section through the notochord at this stage.

The result of this process is that these cartilage rings are eventually transformed into the centra of the vertebræ, becoming hollow at either end and fitting together rim to rim, while the spaces left within the hollow ends of the vertebræ are still filled with the remains of the vanishing notochord (Fig. 424). At the same time a more or less complete system of arches is saddled along the dorsal side of the vertebral column to roof in the nerve cord. This *embryonic* stage of the centra corresponds exactly with the typical condition found in adult elasmobranch fishes, where the vertebræ, which fit together like spools placed end to end, articulate by their centra and are held together in a column by a common sheath.

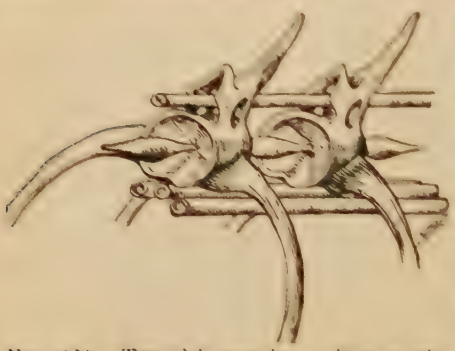


FIG. 424.—Two fish vertebræ, showing the last remains of the notochord. (After Jammes.)

The cartilaginous invasion of the notochord is followed, in teleost fishes, by the downfall of the cartilage itself before the gradual encroachment of bony tissue, transitional stages of this process being shown by the ganoids.

FIG. 425.—Ball and socket vertebræ of an adult alligator, showing the suture between the centrum and neural arch still persisting. (Drawn by R. S. Stites.)

Since in all fishes the ends of the *centra*, whether cartilaginous or bony, are cuplike (Fig. 424), there is little provision for the play of one vertebra upon another. This is, however, sufficient for the reason that so long as life in water is maintained, the prevailing lateral body movement demands only a solid axial foundation for muscle attachment.

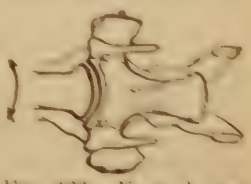


FIG. 426.—Ventral view of one cervical vertebra of a swan, and a part of another, showing a saddle joint, the movement of which is not only in the direction of the arrows but also at right angles to them. (Drawn by K. L. Bardon.)

The end of each antenna is amputated and another generally becomes modified into a hollow-ended pouch which allows a greater freedom of movement (Fig. 62). The "socket" is already at hand, being provided by the method of formation of the antennae as buds. It is only necessary for the intermediate mass of undifferentiated tissue to form the "ball," by filling up and fusing with the top of one end only of each socket, to complete the ball-and-socket device. In antennae not applied as a male clasping organ, as in the antennae and of the ventral process, which is here of a peculiarly common, with the normally being prominently

Another type of antenna, found particularly in the extremely hairy males of birds, is formed by a subtle joint connecting the antennae (Fig. 62). This type of articulation permits movements in two directions at right angles to each other, as in the case of a man using a hollow-ended, saddle horse, clipping and only have side to side, but also rocking forward and backward.

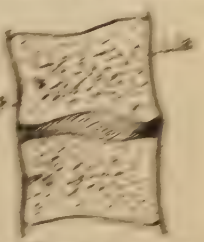


Fig. 62.—A very common method of articulation between the antennae and the head. The antennae are connected to the head by a ball-and-socket joint, which allows movement in all directions. The antennae are also connected to the head by a hinge joint, which allows movement in one direction only. The antennae are also connected to the head by a ball-and-socket joint, which allows movement in all directions.

In connection with the antennae generally it should be noted that in the adult, as well as in the embryo, the articulation of the antennae with each other is largely maintained from the earliest to the metamorphosis, that is, the processes that project from the earlier. Traces of the antennae retained with regard to the antennae of adult mammals in the shape of the median projection (Fig. 62), which forms the central part of the intermediate part of these segments that separate the centre of the antennae from each other.

2. Differentiation of the Antennae

The number of segments in the antennae does not increase with age and growth. On the contrary, as the result of fusion or adult life is frequently decreased. Variations are usually more common in the lower forms than in higher forms. As a rule, for example, may have as many as four hundred segments. It is doubtful whether the number has ever to remain fixed, individuals of a species which would have a larger number of

vertebræ than representatives of the same kind found in more northern waters.

While the separate vertebræ composing the backbone are easily referable to one structural plan, no two are exactly alike. The variations that have arisen are closely correlated with the diverse work which each vertebra, or group of vertebræ, has to do. Thus, since it is desirable to have the head move in any direction without turning the entire body, the vertebræ of the neck which carry the head have developed joints that move more freely than any to be found elsewhere in the skeletal axis. On the other hand, the sacral vertebræ, which bear the weight of the body upon the legs, have lost their movable joints entirely and become fused together into an efficient unit of support. This differentiation, however, is a matter of long evolutionary processes.

The points of attachment of arms and legs, as well as the region where ribs are present, serve as landmarks, dividing the vertebral column of man into six natural groups of vertebræ, namely, cervical, thoracic, lumbar, sacral, coccygeal, and caudal.

In amphioxus and the cyclostomes, as already indicated, there are no separate vertebræ, since the ancestral notochord still holds sway. Among fishes the vertebræ posterior to the anal region develop a hæmal arch on the ventral side of their centra. The spinal column, therefore, may be divided into *trunk vertebræ*, essentially alike, which are anterior to the anus, and postanal *caudal vertebræ* possessing the hæmal arch, and diminishing in size posteriorly.

Practically the same condition exists in amphibians, with a smaller total number of vertebræ involved, except that between trunk and caudal vertebræ there appears a single *sacral vertebra* to which the pelvic bones of the hind legs are attached. The anchorage of the hind legs to this solitary inadequate sacral vertebra, is one of the reasons why amphibians are unable to "stand," or bear their weight upon their hind legs.

Among reptiles the differentiation of the vertebræ includes several advances. Excepting snakes and footless lizards every reptile has *two sacral vertebræ* for the attachment of the pelvic girdle and the support of the hind legs, while the trunk vertebræ become specialized at either end into *cervical* and *lumbar vertebræ* respectively. The remaining trunk vertebræ, between the cervical and lumbar vertebræ, to which the ribs encircling the body

cavity are now attached, are termed *thoracic vertebræ*. Not all reptiles, however, are equally diversified with regard to vertebræ. Snakes, for example, lack both cervical and sacral vertebræ with the result that the entire column presents a uniformity suggesting that of fishes, except that the trunk vertebræ, with their well formed ribs, are more properly thoracic in character.

The vertebræ of birds undergo great modification in connection with adaptation for flight. The caudal vertebræ become much reduced and crowded together; the sacral vertebræ now successfully bearing the entire weight of the bird by reason of substantial additions from both sides of the lumbar region, fuse into a large firm sacral bone; the lumbar vertebræ become comparatively few because of these contributions to the sacrum; the thoracic vertebræ develop elaborate processes whereby they are securely interlocked and tied together by ligaments; while the cervical vertebræ reach the highest number and much differentiation. A flexible neck is a prime necessity for a bird, which has no hands and must pick up all of its food with a prehensile beak. Even such a bird as an owl, which apparently has a short neck, can turn its staring eyes in any direction not only with the greatest ease but also without any disturbance to its immobile body.

In mammals the cervical vertebræ number seven, whether the neck is functionally absent, as in whales, or conspicuously present, as in the bizarre giraffes. There are four known exceptions to this rule. The three-toed sloth, *Bradypus*, has nine cervical vertebræ; the ant bear, *Tamandua*, eight; while the two-toed sloth, *Cholœpus*, and the American sea cow, *Trichechus*, each have six.

The first two cervical vertebræ are further specialized into the so-called atlas and axis. The *atlas* takes its name from human anatomy since in man it "bears the weight of the world" in the form of the head upon its shoulders, after the fashion of its mythical prototype. Two articular surfaces at the base of the skull in mammals, the *occipital condyles*, are in contact with two corresponding surfaces on the atlas, thus forming a joint that allows for nodding movements of the head. The atlas is virtually without the neural spine of a typical vertebra, and has also lost its centrum. Its neural arch, however, is relatively large, and, with a substitute bridge of bone where the true centrum ought to be, forms an open ring (Fig. 428).

The second cervical vertebra, or *axis*, has a double centrum, its

own and the lost centrum of the axis which is fused with it, forming a large process, the *odontoid process*, that projects towards the head. The odontoid process rocks back and forth and from side to side upon an articular surface within the ring of the atlas, thereby allowing lateral movements of the head. That this large process is really the transformed centrum of the atlas, is borne out by two facts. First, it is in the position of the missing centrum of the atlas, and second, in fetal life, it is entirely separated from the axis. Furthermore, it is formed embryologically around the notochordal core in the same way that centra of other vertebræ are.

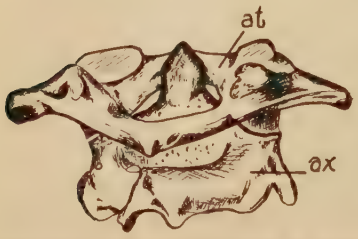


Fig. 428.—The human atlas, *at*, and the axis, *ax*. (After Sobotta and McMurrich.)

In the human embryo there are present seven cervical, twelve thoracic, five lumbar, five sacral, and four or five, or sometimes as many as eight caudal vertebræ. In the adult the five sacral vertebræ fuse to form a single sacral bone, and usually all the caudal vertebræ are joined to make the coccyx, although it is not very exceptional for one or two of the most posterior caudal vertebræ to retain their independence. Occasional tails of several inches in length and containing caudal vertebræ, have been authentically reported as occurring in adult human beings.

The differentiation of vertebræ in the vertebrate series is visualized diagrammatically in Figure 429.

4. The Vertebral Column

The units of the vertebral column taken together are more differentiated at either end of the vertebral column than they are in the middle. In the higher vertebrates notable specialization of the cervical vertebræ is correlated with use, while the degeneration of the caudal vertebræ is apparently an expression of disuse.

The entire skeletal axis has in general three uses, namely, support, protection of the nerve cord, and movement.

A. Support

The function of support is what may be called the "backbone" function. In other words it is the furnishing of the cor-

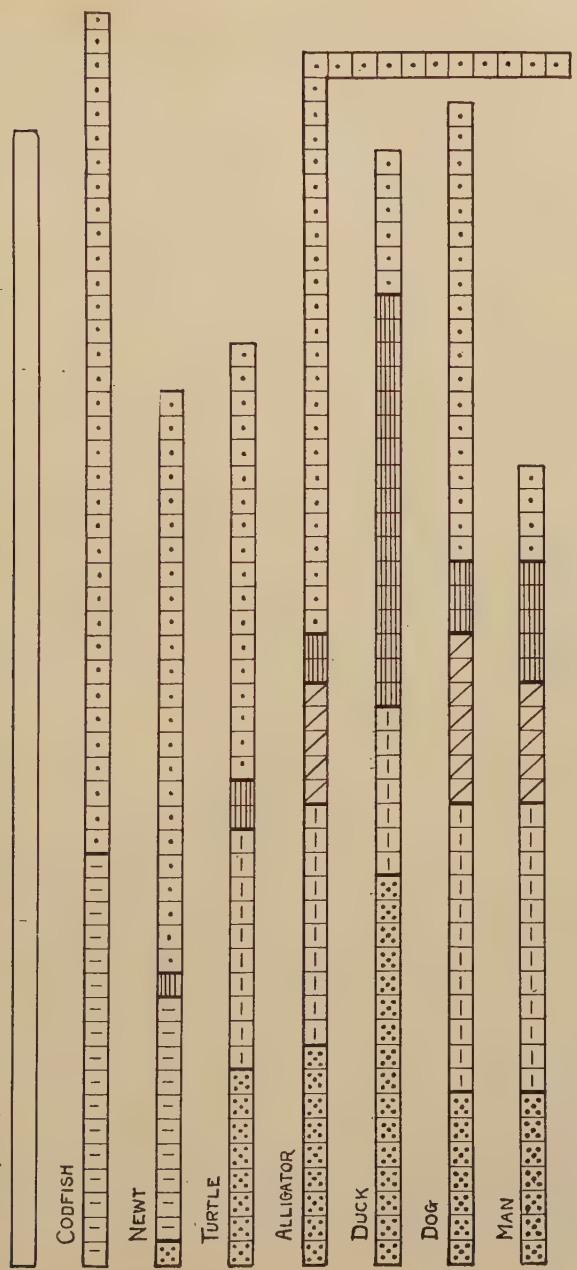


FIG. 429.—Diagram of the differentiation of the vertebræ in representative vertebrates.

ner stone upon which the other parts of the body are built. This solid foundation is arranged lengthwise the body along its longest axis, because in this way the greatest number of parts of the body can conveniently be accommodated with a sustaining anchorage.

In animals like man that tip up on end and poise a heavy head on top of the vertebral column, the function of support is more effectually accomplished because of certain adaptive curvatures in the backbone, which make the column mechanically more flexible than a straight shaft would be. These curvatures, which are due more to modifications of the padlike fibrous cartilages between the separate vertebræ than to any direct change in the shape of the centra that are stacked one upon the other, are less pronounced in infants and in primitive races than in adult civilized man. This is particularly true of the lumbar curvature (Fig. 430), that gives the typical hollow back to a well-formed man. Babies, which lack it, are flat-backed, like their remote quadrupedal ancestors.

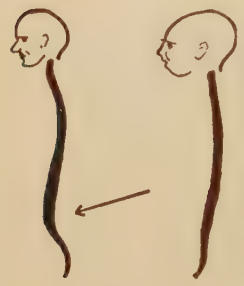


Fig. 430.—Diagrams showing the difference in the curvature of the backbone between an infant and an adult.

B. Protection of the Nerve Cord

The nerve cord in vertebrates is an indispensable cable of great complexity, extremely delicate and liable to injury. It is not only ensheathed in its own envelopes, the pia mater, arachnoidea, and dura mater, but it is also surrounded by a protective jacket of fluid and is furthermore encased within a bony conduit formed by the neural arches of the vertebræ. Even the backbone itself is overlaid with ligaments and buried with its valuable contents protected from outside injury by surrounding muscles and fatty tissues. Finally the whole internal mechanism is effectually sealed up within the tough, resistant, practically germ-proof skin.

C. Movement

Vertebral movement along the spinal column, while relatively slight between any two vertebræ, when taken all together, amounts to enough to be greatly missed by anyone afflicted with a stiff neck or a lame back.

In turtles movement is confined to the cervical and caudal regions, but in snakes it is uniformly possible along the entire length of the body.

Caudal movements alone serve a great variety of uses, such as locomotion in fishes, support in kangaroos, prehension in long-tailed monkeys, balancing in cats, insect removal in horses, and the expression of the emotions in dogs.

III. THE THORACIC BASKET

1. In General

The vertebral column has to do with the tubular dorsal nerve cord. The other of the two essential tubes that characterize the vertebrate body, namely, the digestive tube, is encircled and protected, at least partially, by another part of the skeleton, the *thoracic basket* (Fig. 293), which consists primarily of the thoracic vertebræ, the ribs, and the breastbone, with the pectoral girdle sometimes playing a supplementary rôle.

The thoracic basket first appears in connection with life on land in the class Reptilia, where a true breastbone and encircling ribs are present. This combination of bones, which is hung upon the anterior part of the skeletal axis, not only encloses a considerable part of the digestive organs, but also furnishes protection to other soft viscera, notably the heart and lungs, that are in great need of skeletal protection. In the higher vertebrates still other organs, originally contained within the thoracic basket, have lost this protection, either by the contraction or the degeneration of the structure itself, thus exposing the part to be protected. This is particularly true with organs in the posterior part of the body cavity, like the small intestine, much of which is exposed, or the kidneys and gonads that have migrated tailward from their original embryonic or ancestral position within the basket.

The thoracic basket is marked off at either end by a more or or less transverse top and bottom in upright man, while the sides are made up of skeletal elements embedded in muscular walls. The top of the basket is a rather restricted area, whose margin is determined by the first thoracic vertebra, the first pair of ribs, and the upper end of the breastbone (Fig. 431). This area limits a narrow passage-way through which there are crowded

side by side various structures, providing for much of the traffic between head and trunk (Fig. 432). These structures include the *trachea*, connecting the imprisoned lungs with the outside world; the *esophagus*, that passes on food and drink, placing it safely beyond normal recall; the *vagus nerves*, wandering far from their headquarters in the brain to supply distant viscera; the *carotid arteries* and *jugular veins*, which distribute and collect the blood in the head; and the *thoracic duct*, that brings back into the confines of the venous system escaped white blood cells from their peregrinations throughout the tissues of the body.

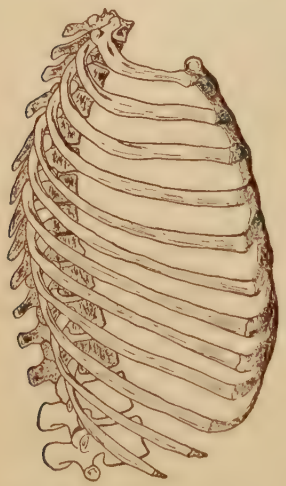


FIG. 431.—The thoracic basket. (After Spalteholz.)

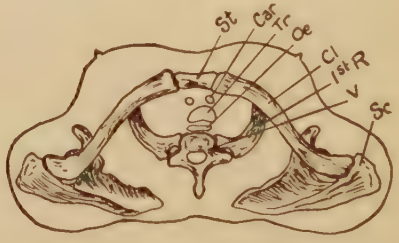


FIG. 432.—Diagram of the opening at the top of the thoracic basket, as seen from above. *St*, sternum; *Car*, carotid artery; *Tr*, trachea; *Oe*, esophagus; *Cl*, clavicle; *1st R*, first rib; *v*, vertebra; *Sc*, scapula. (After Witkowski.)

The floor of the basket in man is larger than the top, and is bounded behind by the last thoracic vertebra together with the short twelfth pair of ribs attached thereto. On the sides and in front the margins of the floor are determined by the tips of the tenth and eleventh pairs of ribs, and the cartilages of other posterior ribs which attach them to the breastbone, as well as by the lower end of the breastbone itself. The floor is closed crosswise by the vaulted diaphragm, and tends to slope downward from the sternum towards the backbone, while the plane of the smaller top of the basket slopes upward toward the backbone, since the sternal side is shorter than the vertebral side. In general the form of the whole basket is somewhat cone-shaped in man, with the smaller upper end toward the head.

The space within is partially divided into right and left por-

tions projecting dorsally like bay windows from the general cavity, because the column formed by the centra of the vertebræ, stacked one upon the other, stands out into the cavity, thus serving to a certain degree as a longitudinal partition. Within these lateral enlargements are packed the lungs, while the heart lies midway between the lungs instead of far over on the left side as melodramatic actors are wont to indicate.

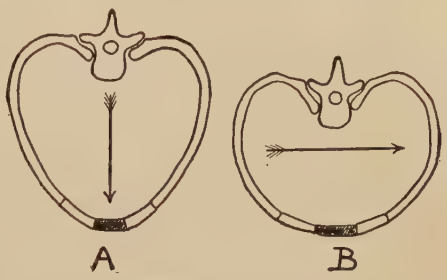


FIG. 433.—Cross sections through the thorax of, *A*, a human embryo, and *B*, a human adult. The former resembles that of a quadruped. (After Wiedersheim.)

Compared in cross section, the shape of the thorax of the human embryo is seen to be decidedly different from that of the adult (Fig. 433). In the embryo the dorso-ventral diameter exceeds that from side to side. In the human adult, on the contrary, where the visceral weight exerts a pull parallel to the backbone rather than at right angles to it, the greater diameter of the basket is no longer dorso-ventral, but from one side to the other. Quadrupeds resemble the human embryo in the relative dimensions of the thoracic basket, this condition being correlated with the weight of the viscera, which pulls mechanically from the backbone downward towards the sternum.

2. Ribs

The ribs, which have been of particular human interest ever since the days of the Garden of Eden, are the most conspicuous part of the thoracic basket. They vary in length from mere movable tips attached to the transverse processes of the vertebræ, to bands of bone encircling the body. Primitively, there is a pair of ribs for every vertebra from axis to sacrum, whenever these landmarks are present, and some fishes even have two pairs. The general tendency, however, is towards a reduction in number at either end of the series.

Ribs may form in the sheaths of connective tissue that separate the metameric muscles of the body wall from each other, and secondarily become connected with the vertebræ, or they

may grow out from the vertebræ themselves, since the ribs of all animals are not homologous structures.

A. Human Ribs

A typical human rib is a flattened bone both bent and twisted so that it cannot be made to lie flat when placed upon a table (Fig. 434). Its slender, somewhat elastic body is pieced out at the sternal end with flexible cartilage. At the dorsal end, which joins the thoracic vertebræ in two places, are two prominences, known as the *head* and *tubercle* respectively, and separated from each other by the *neck*, which is slightly narrower than the *body* of the rib. Both head and tubercle bear articular facets by means of which the rib plays upon its vertebral support.

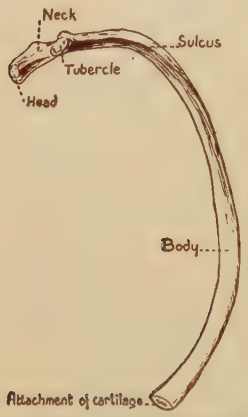


Fig. 434.—The fifth right bony rib, seen from below. (After Cunningham.)

There are twelve pairs of ribs in man (Fig. 431), although much evidence from comparative anatomy and embryology supports the conclusion that the ancestors of modern man had more. That reduction is going on is evidenced by the degeneration of the ribs in the posterior region of the thoracic basket where at least two pairs fail to reach the sternum.

To understand the nature of this degeneration it should be stated that all ribs articulate at one end with the thoracic vertebræ, while at the other end only the first seven pairs, or *true ribs*, join the sternum. The remaining five pairs are known as *false ribs*. Of these the eighth, ninth, and tenth pairs anchor indirectly to the sternum by means of the cartilages of the seventh pair of true ribs, while ordinarily the eleventh and twelfth pairs, which are called *floating ribs*, have so far degenerated that they only partially encircle the body, thus failing to make even a vicarious attachment to the sternum. The ribs of man, therefore, increase in length from the first to the seventh or eighth pairs, and then successively decrease to the twelfth pair, which may be reduced to mere stubs hardly more than an inch long.

In medical literature numerous cases are cited of extra human

ribs persisting in adult life either at the cervical or lumbar ends of the thoracic series. Pilling gives an instance of a pair of ribs on the seventh cervical vertebra that completely encircled the upper area of the thoracic basket and joined the sternum, quite in the manner of true ribs (Fig. 435). Persistent cervical ribs, however, are more frequently incomplete and fail of direct sternal attachment. Even the first pair of thoracic ribs may sometimes be incomplete (Fig. 436). Additional ribs are of more frequent occurrence on the first lumbar vertebra, than in the cervical region. An extra pair of lumbar ribs are called the "gorilla ribs" because they represent the normal condition in gorillas and chimpanzees. Rabl examined 640 bodies in the dissecting rooms of the University of Prague and found 40 of them, or a little more than 6%, with a gorilla rib on at least one side. Incidentally it is interesting to know that two out of the 640 had only eleven pairs of ribs. Gorilla ribs are about three times more frequent in the male than in the female, a fact difficult to harmonize with Adam's historic loss.

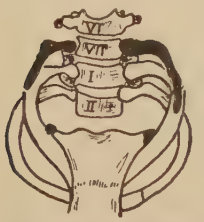


FIG. 435.—Abnormal ribs (in black) on the seventh cervical vertebra of an adult individual. (After Leboucq.)

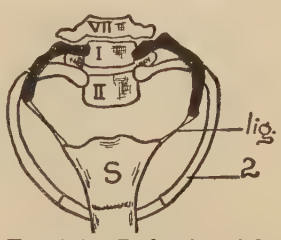


FIG. 436.—Reduction of the first pair of ribs (in black) in an adult individual. *lig.*, ligament; *S*, sternum; *2*, second thoracic rib; *VII*, seventh cervical vertebra; *I*, *II*, first and second thoracic vertebræ. (After Leboucq.)

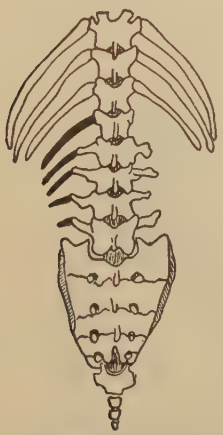


FIG. 437.—A part of the thoracic vertebræ; the lumbar vertebræ; the sacrum; and the coccyx, with embryonic lumbar ribs, represented on one side in black. (After Wiedersheim.)

With respect to length the eleventh pair of floating ribs varies from six to eleven inches, while that of the twelfth pair ranges from mere stubs to ribs which nearly encircle the body, or from less than an inch to about a foot in length.

Finally, in fetal life, ribs are temporarily present not only upon the seventh cervical vertebra but also upon all the lumbar vertebræ (Fig. 437). Moreover, rudiments of ribs

which afterwards fuse with the transverse processes to form the lateral masses of the sacrum, are attached to the sacral vertebræ (Fig. 438).

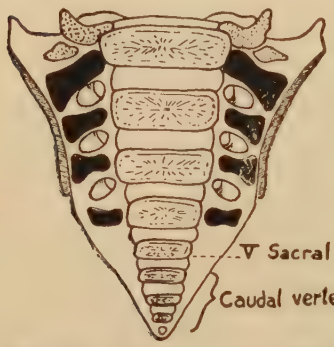


Fig. 438.—Sacrum of a human fetus five months old, showing sacral ribs, in black. (After Kollmann.)

B. Comparative Anatomy of the Ribs

The ribless vertebrates include amphioxus, the cyclostomes, holocephalans, skates, and the lophobranchs, such as *Sygnathus* and *Hippocampus* under the teleosts. In the ganoid *Polyodon* also, the ribs are quite vestigial.

Among other fishes there are two sorts of ribs of different origin, namely, hæmal and pleural, both of which are connected at one end with the vertebral column and unattached at the other (Fig. 439). *Hæmal ribs*, which are the more primitive, represent simply hæmal arches anterior to the anus, that have spread enough to partly encircle the body cavity. They con-

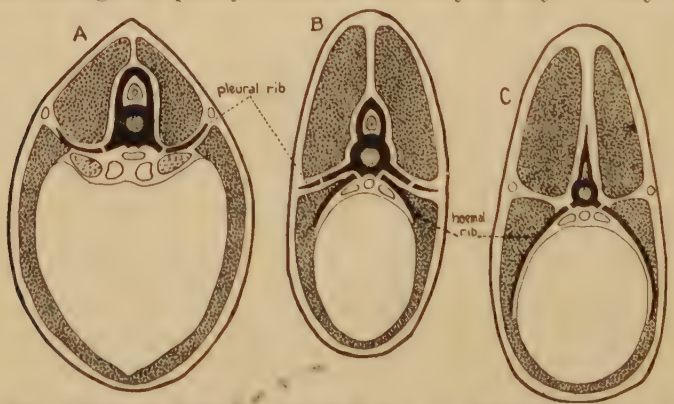


Fig. 439.—Diagrams of the three types of ribs. *A*, elasmobranch with pleural ribs; *B*, ganoid with both pleural and hæmal ribs; *C*, teleost with hæmal ribs. (After Cöppert.)

sequently lie entirely inside the muscles of the body wall, next to the peritoneal lining of the cœlome, and are, therefore, termed appropriately "ventral ribs." The ribs of the dipnoi, as well as of most teleosts and ganoids, are of this character.

Pleural ribs, on the other hand, grow out from the transverse processes of the vertebræ and extend between the inner and outer sheets of muscle that form the body wall. They are thus called "dorsal ribs" in contrast to the ventral ribs. Most elasmobranchs, together with all vertebrates above fishes, have pleural ribs. In elasmobranchs, as well as amphibians, the pleural ribs are short and insignificant, but beginning with reptiles, they become longer, in many instances encircling the body cavity and joining at the ventral ends with the sternum to form a complete thoracic basket.

There are a few fishes, notably the ganoid *Polypterus* and certain clupeoid and salmonoid teleosts, which have both hæmal and pleural ribs, one outside the other (Fig. 439, B), making two pairs of ribs to each vertebra. These fishes are consequently connecting links in the evolutionary story of the ribs.

Fig. 440. — A vertebra with two ribs (in black) of a salamander, showing the primitive double articulation of ribs to vertebræ. (After Gegenbaur.)

Amphibian ribs are pleural in type. Although they are never prominent, in urodeles they are present even on the caudal vertebræ, and in no modern amphibian do they encircle the body cavity. The fossil stegocephalans had strong well developed ribs, but there is considerable doubt whether these ancient animals were the ancestors of amphibians living today. If they were, the ribs of modern amphibians are to be regarded as vestigial rather than primitive structures.

The ribs of urodeles are forked like a letter Y, thus having two points of attachment to the vertebra (Fig. 440), forming a passage-way between the fork and the vertebra, called the *foramen transversarius*. This still persists even in human ribs, where one branch of the fork becomes the "head," and the other the "tubercle" of the rib (Figs. 434 and 441).

The ribs of anurans are not forked, and appear as small, insignificant, movable tips attached to the transverse processes of the vertebræ.

Among reptiles the ribs found in lizards and crocodiles are most typical, becoming differentiated into a dorsal, bony, vertebral part, homologous to the rib of the urodele, and a cartilaginous, ventral sternal part, which is something entirely new

in skeletal devices. Some lizards and crocodiles even have a third bony part intercalated between these two.

Since there is no sternum in snakes, all the ribs are "floating," which makes it possible for them to aid in locomotion, as a snake grips the ground with its ventral scales and the ends of the movable floating ribs. Turtles do not have sternal elements in their ribs. Instead the vertebral parts of the ribs flatten out and join together with dermal *costal plates* forming the shell (Fig. 442).

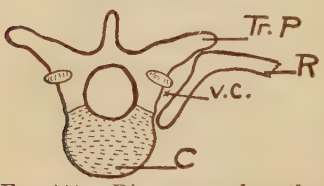


Fig. 441.—Diagram to show the articulation of, *R*, a rib on the centrum, *C*, and on the transverse process of a vertebra, *Tr.P*, thus forming the vertebrarterial canal, *V.C.* (After Weber.)

In *Sphenodon*, the "living fossil" lizard of New Zealand, there are several unusual ribs in the tail region, which suggests an ancestral prodigality of ribs.

As might be expected, birds present extreme modifications in their ribs. Both the vertebral and sternal parts are present and entirely ossified, making a firm thoracic basket for the attachment of flight muscles. This firmness is further enhanced since most of the ribs are "true," that is, connected with the sternum, while the ribs in the sacral region fuse with vertebræ to form a large, strong "back-piece," or sacrum. Moreover the ribs of birds are thin and flat, affording surface for muscle attachment, and in addition are provided with supplementary cross bones, or *uncinate processes*, (Fig. 416), which serve to weld the thoracic basket together into a firm resistant unit for muscle attachment. In *Archæopteryx*, the oldest known bird, the ribs were rounded like those of lizards, instead of flat, and were without uncinate processes.

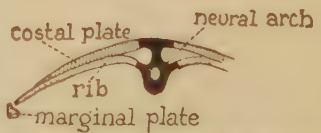


Fig. 442.—Cross section through the carapace of a turtle. (After Huxley.)

In mammals the ventral, sternal part of the ribs remains cartilaginous, and the total number varies from nine pairs in the bottle-nosed whale, *Hyperodon*, to twenty-four pairs in the two-toed sloth, *Cholœpus*.

True ribs that reach the sternum directly, vary from two pairs in the manatee, *Trichechus*, to ten pairs in the spider monkey, *Ateles*.

3. Sternum

As contrasted with the backbone, the *sternum* or "front bone," is the terrestrial part of the thoracic basket, that is, it appears first in evolutionary history in vertebrates that locomote upon land. The need of such a strengthening structure to knit together the whole thoracic basket into a firm skeletal unit to which the muscles of the anterior legs, or arms, may find suitable anchorage, is not felt by such primitive water dwellers as fishes, that go forward by lateral tail motion rather than by the leverage of bilateral appendages. There is also no need among the lower vertebrates for a skeletal piece corresponding to the sternum, in connection with the pelvic girdle and the posterior pair of legs, because this apparatus, unlike the case of the pectoral girdle and the anterior pair of appendages, articulates at the sacrum directly with the vertebral column.

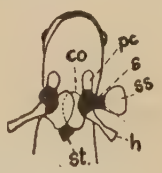


FIG. 443.—Diagram of the pectoral girdle of a salamander. *co*, coracoid; *pc*, procoracoid; *h*, humerus; *s*, scapula; *ss*, supra-scapula; *st*, archisternum. (After Wiedersheim.)

The true sternum, *neosternum*, is introduced into the vertebrate series with the reptiles, but certain other skeletal, although not homologous, structures appear along the ventral wall of the body, either before, or at the same time with, the establishment of the neosternum. These structures are variously designated as the archi-, omo-, xiphi-, para-, and episterna.

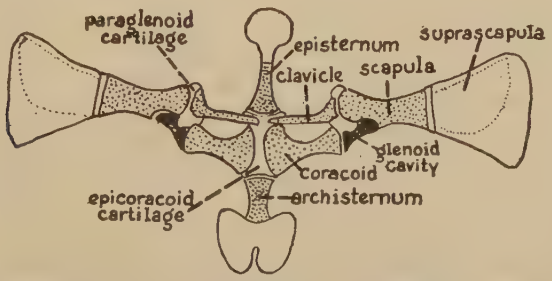


FIG. 444.—Ventral view of shoulder girdle and sternal apparatus, flattened out, of a frog. (After Gaupp.)

Not only are fishes without any kind of sternal structures, but also some of the lowest urodeles, as *Proteus* and *Amphiuma*. The apodans, snakes, and turtles are deficient in the same manner.

In higher urodeles the intermuscular connective tissues along the ventral region between the front pair of legs gives way to a cartilaginous formation of a primitive skeletal element, known as the *archisternum* (Fig. 443). The indefinite and irregular beginnings of this structure, according to Wilder, appear even in the mud puppy, *Necturus*. The archisternum is entirely out of touch with the vertebral column, for there are as yet no ribs of sufficient length to span the distance.

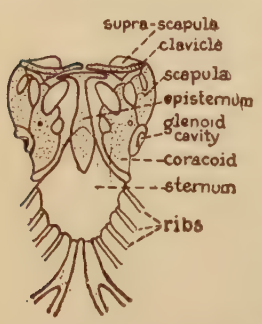


Fig. 445.—Fenestrated shoulder girdle of an iguana. (After W. K. Parker.)

In the anurans the archisternum reaches its greatest development and becomes a definite skeletal structure, incorporating with itself on either side the pectoral girdles which bear the front legs (Fig. 444). The main part of the archisternum in toads becomes bony, with an expanded posterior, cartilaginous appendage, called the *xiphisternum*, while in frogs still another skeletal element, the *omosternum* is added anteriorly, making altogether a continuous, median, skeletal support for the front legs. The whole sternal complex is held in place by muscles rather than by any articulation with the backbone, so that when these muscles are severed, the entire apparatus, together with the attached front legs, may be slipped off over the head, like a ring off a finger, without parting a single joint or articulation. Since the hind legs of an amphibian are connected with the backbone only at a single sacral vertebra, it will be seen that they are very inadequately related to the axial, skeletal foundation, which fact explains in part the awkward and inefficient manner of amphibian locomotion.

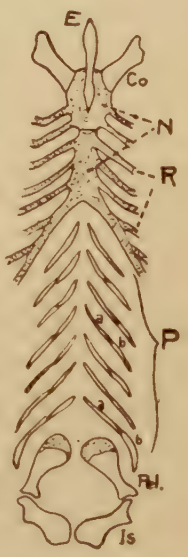


Fig. 446.—Breastbone and parasternum of alligator. *E*, episternum; *Co*, coracoid; *N*, neosternum; *R*, ribs; *P*, parasternum; *a* and *b*, separate elements of parasternum; *Pel.*, pelvis; *Is*, ischium. (After Gegenbaur.)

In addition to the neosternum, which is laid down primarily as cartilage to be later replaced by bone, there is an extra T-shaped median plate of bone, in the Crocodilia and certain lizards, which

is formed directly in connective tissue, and overlaps the neosternum (Fig. 445). This is the *episternum*. The episternum occurs also in the Stegocephali and many fossil reptiles, reappearing in the monotremes among mammals. It may possibly be the homolog of a part of the plastron of turtles.

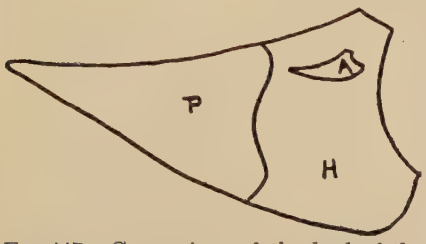


Fig. 447.—Comparison of the keel of the albatross, *A*, pigeon, *P*, and, hummingbird, *H*, supposing all to have an equal spread of wing. (From Beebe, after Lucas.)

A further skeletal support is developed in the Crocodilia, whose heavy bodies rest much of the time directly upon the ground. This is the *parasternum*, or "abdominal ribs," which consists of a series of paired slatlike bones, formed between the muscles on either side of the middle line, posterior to the thoracic basket (Fig. 446). No doubt such a bony grillwork furnishes skeletal support for the belly of these heavy beasts, as it is dragged over the ground.

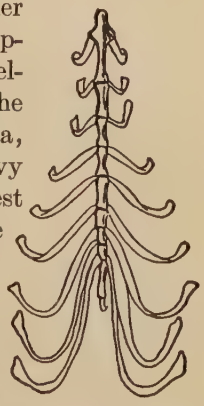


Fig. 448.—The sternum and rib cartilages of a wolf, showing separate sternebræ. (After Scott.)

Birds have an enormously flattened bony neosternum that affords attachment for the pectoral muscles of flight. It is comparatively flat in running birds (Ratitates), but in all other groups (Carinates), a keel, or *carina* as already mentioned, furnishes additional surface for muscle attachment. The carinæ on the breastbones of an albatross, a pigeon, and a hummingbird, drawn to the same scale in Fig. 447, show how large a relative surface for muscle attachment is necessary in the case of the tiny hummingbird in order to maintain its marvellous vibrating wing movement, which is so rapid that the wings themselves may

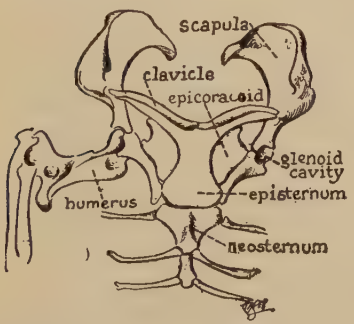


Fig. 449.—Pectoral girdle of *Ornithorhynchus*. (Drawn from specimen in the collection at Brown University by Dorcas Hager.)

blend out of sight, like the spokes of a rapidly moving wheel. A carina is also characteristic of the extinct flying reptiles (Pterodactyls), as well as of flying bats among mammals.

FIG. 450.—The adult human sternum. *M*, manubrium; *G*, gladiolus; *X*, xyphoid process. (After Spalteholz.)

The neosternum, or breastbone, of mammals is formed embryologically by fusion of the cartilaginous tips of the ribs. These elements may ossify into a common median plate of bone, or they may, as is usually the case, form a series of bony *sternebræ* (Fig. 448), alternating with the cartilaginous ends of the ribs. In monotremes the neosternum is reinforced by a T-shaped episternum (Fig. 449), thus harking back to reptilian forebears.

In the human adult, the sternum consists of three parts, namely, the *manubrium* or head, the *gladiolus* or body, and the *xyphoid cartilage* (Fig. 450). Of these the first two are formed of bone and the last of cartilage, as its name implies. In the human embryo the sternum is formed by a double chain of elements, made up at first of cartilage and later of bone, contributed from the sternal ends of the ribs (Fig. 451). These elements eventually fuse together to make the adult structure. Further confirmation of the bilateral origin of the sternum is found in the fact that two parallel centers of ossification occur in the bony part of the sternum (Fig. 452), while the xyphoid cartilage is frequently forked, or perforated by a functionless foramen.

Sixteen articular surfaces are present on the human sternum (Fig. 450), twelve along the sides for the cartilages of the true ribs excepting the first pair which is fused to the sternum; two upon the manubrium for the clavicles or collar-bones; one between the manubrium and the gladiolus; and one between the gladiolus and the xyphoid cartilage.

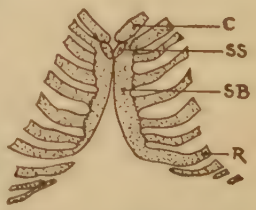


FIG. 451.—Ventral view of the developing sternum of a human embryo, 30 mm. in length. *C*, clavicle; *SS*, suprasternal cartilage; *SB*, sternal bar; *R*, seventh rib. (After Ruge.)

The shortening of the human sternum which results in a conspicuous notch on the front side of the thoracic basket follows the fusion of the *sternebræ*, that is the separate embryonic bones that

make up the sternum, and the consequent disappearance of the intersternebral cartilages.

IV. THE SKULL

The skull in the highest vertebrates is a double structure, embryologically, morphologically, and physiologically. *Embryologically* it is made up of two sets of bones of diverse origin, an outer and an inner, which envelop the brain, supplementing each other. In the course of development these bony elements fuse together into an unified whole. *Morphologically* one skull, the *neurocranium*, surrounds the brain end of the neural tube, while another, the *splanchnocranium*, similarly encircles the anterior end of the splanchnic tube, or digestive tract (Fig. 227). *Physiologically* the two fundamental functions of support and protection are both provided for by the skull, so that it may be said to serve a double purpose.

Fig. 452.—Sternum of a child, showing centers of ossification. Seven ribs are attached on the right side and eight on the left. (After Markowski, in Kollmann's Atlas.)

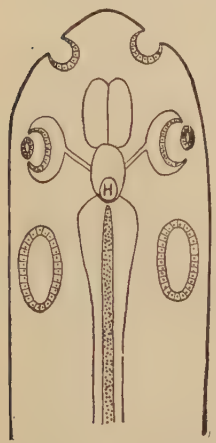


Fig. 453.—Diagram of the notochordal stage of skull development, seen from the ventral side. The notochord (dotted) lies along the nerve cord and brain as far forward as *H*, the hypophysis. Three pairs of sense organs, nose, eye, and ear, have appeared, but as yet are without skeletal support. (After Wilder.)

1. The Evolution of the Brain Case

A composite moving picture of the rise and union of these two embryonic skulls may, for clearness of description, be divided into a series of stages that pass continuously from one into another. Many of them, which are largely represented in the adult condition of various vertebrates, extinct as well as living, are found, in counterpart at least, during the development of the human skull, although the parallel is by no means exact.

A. Notochordal stage

Just as the brain develops after the spinal cord, so the first evidences of a future skull do not appear until after the notochord

is well established. Before any skeletal elements except the notochord are present, a thin, tough, membranous sac surrounds the brain, which later is replaced by the *dura mater* and the roof of the skull. There are also present three pairs of conspicuous sense organs arranged one behind the other along the sides of the brain. These are the *olfactory pits*, the *eyes*, and *ears* (Fig. 453). At this stage the anterior enlargement of the nerve cord in the form of the brain extends horizontally in front. Although in need of support it is as yet quite unprovided for skeletally since the diminishing notochord does not extend far enough forward and is not of the right shape, to make a platform upon which it may rest.

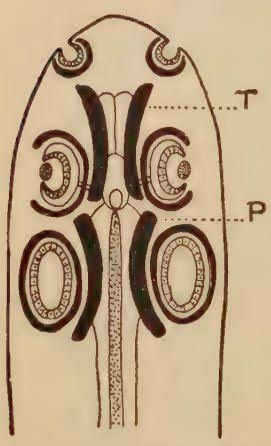


Fig. 454.—Diagram of the underpinning stage of skull development, seen from the ventral side. The brain now rests upon *T*, the trabeculæ, and *P*, the parachordals, while each pair of sense organs is supported by skeletal parts (in black). (After Wilder.)

B. Underpinning Stage

This need is soon met, however, by the appearance of two pairs of independent flat cartilages which form a primitive underpinning, or floor for the support of the rapidly developing brain. One pair of these cartilages, the *parachordals*, is placed under the brain, with their posterior ends lying on either side of the notochordal tip end, while the position of the other pair, the *trabeculæ*, is more anterior (Fig. 454). Delicate cartilaginous capsules, meanwhile, enclose the three pairs of sense organs.

C. Fusion Stage

The four primitive girders thus laid down are at first quite independent, not only of each other but also of the end of the notochord, and the six sense-organ capsules. Marginal growth speedily results, however, in their coming into contact and eventually coalescing as a single continuous platform which encloses at its posterior end the tip of the notochord, and along its lateral margins the capsules of the sense organs (Fig. 455).

The manner of fusion of this platform with the sense-organ capsules is different in the case of each, due to the fundamental difference in the kinds of stimuli that the various sense organs are

destined to receive. Thus, the inner ear, which is attuned to respond to vibratory contact of sound waves that can be transmitted even through an enveloping case, is entirely surrounded by skeletal cartilage. The eyeball capsule, on the other hand, which needs to rotate freely in order to be directed toward vibrations of light coming from any direction, does not fuse with the rest of the skull but retains its independence, fitting within a socket, or orbit, formed in the wall of the skull. Consequently the primitive skeletal capsule of the embryonic eye eventually becomes the tough, outer, sclerotic coat of the eyeball. Finally, the capsules of the olfactory pits fuse solidly on their posterior and inner surfaces with the skull itself, although perforated by the olfactory nerves. On their outside surface they remain open like cups for the reception of odorous gases, for these, in order to produce a reaction, must come into direct chemical contact with the nerve endings of smell within the cup.

Fig. 455. — Diagram of the fusion stage of skull development, seen from the ventral side. The parachordals and trabeculæ have fused together into a continuous platform involving the cartilage supports of the nose and ears, and the end of the notochord, while those of the eyes remain independent in the form of the sclerotic layers of the eyeballs, thus making possible the movement of the eyeballs within the orbits. (After Wilder.)

D. Up-Growth Stage

The platform thus formed by fusion serves not only for support, but also as a protection to the brain on its under side. The protective function is soon enlarged to include the sides of the brain by the up-growth of the platform at its margins between the sense organ capsules (Fig. 456). In this stage the skull somewhat resembles a deep spoon, in the bowl of which the brain lies.

Fig. 456.—Up-growth stage of skull development, as seen from the side. (After Roule.)

E. Roofing-Over Stage

Growth at the margin of the developing cartilaginous skull case continues until the edges meet above and fuse together, thus completing, at least in primitive vertebrates, a protective skeletal envelope on all sides of the brain. For example the skull of the dogfish, *Mustelis* (Fig. 457), is a continuous cartilaginous casket enveloping the brain, with no sutures to demark separate elements. It is pierced by various small foramina through which the cranial nerves find exit, as well as by a large posterior opening, the *foramen magnum*, through which the nerve cord enters. It frequently happens particularly among higher vertebrates like man, that the roofing over is not accomplished with cartilage in the manner here described as characteristic for the primitive skull of elasmobranch fishes.

Fig. 457.—Dorsal view of the skull of a dogfish, showing a continuous cartilaginous capsule without sutures.

Thus far only the formation of the *inner skull* has been touched upon. The stages that follow concern the origin of the *outer skull*, and the final modification and fusion of the two skulls into one.

Fig. 458.—The skull of a sturgeon, *Acipenser*, showing the inner cartilaginous skull (dotted) and the outer skull of bony scales. (After Gegenbaur.)

F. Shingling Stage

After the formation of the inner cartilaginous envelope just described, or even before that process is complete, the skull becomes partially overlaid with certain definite bony elements, which are not at first formed in cartilage. These do not ordinarily fuse together so as to lose their identity, but instead join each to the other by means of clearly defined, immovable joints, or sutures, and they together constitute the *outer skull*.

In cartilaginous ganoid fishes, such as the sturgeon, *Acipenser* (Fig. 458), these outer bones are small, numerous, and quite scale-

like in character. In fact they *are* scales that cover the head and are in no essential way different, except in their somewhat enlarged size, from neighboring scales that cover the body. The outer skull, therefore, makes its initial appearance as an armor of separate scaly plates, loosely shingled over the inner cartilaginous brainbox.

G. Ossification Stage

Centers of ossification soon appear in the inner skull, however, particularly around the foramina for the exit of the nerves, where protection is especially needed. What was formerly a continuous cartilaginous sheath for the brain thus becomes gradually replaced by definite bones, which increase rapidly at their margins and so allow the entire structure to accommodate itself to the enlarging brain within. Finally the new bones of the inner skull, like the scaly bones of the outer skull, join together in sutures. Skulls in this stage of development occur principally among the bony ganoids, of which the bowfin, *Amia* (Fig. 459), is a representative. The process of ossification of the inner skull is more completely carried out in amphibians and reptiles.

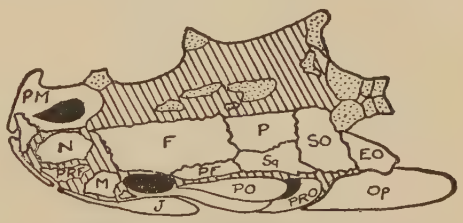


Fig. 459.—Skull of a ganoid fish, *Amia*, as seen from the dorsal side, with the investing bones removed from the right half. (*Investing* bones in white; cartilage in parallel lines; *replacing* bones, ossifying out of cartilage, dotted.) *PM*, premaxillary; *N*, nasal; *PRF*, prefrontal; *M*, maxillary; *F*, frontal; *PF*, postfrontal; *J*, jugal; *PO*, postorbital; *PRO*, preopercular; *Op*, opercular; *Sq*, squamosal; *P*, parietal; *SO*, supraoccipital; *EO*, exoccipital. (After Bütschli.)

H. The Union Stage

The outer skull bones next sink deeper in from their former scalelike position, and, becoming overlaid with skin, are grafted inseparably to the bones of the inner skull. A single skull is now all that is visible, for there is no way, except by tracing the mode of origin, to distinguish the *investing bones* of the outer skull from the *replacing bones* of the inner skull, since both present the same appearance. This embryonic stage of the union of the outer and inner skulls, is similarly represented in the evolutionary series of amphibians and reptiles.

The two skulls are not brought in all cases into such close contact with each other that the dual character of the vertebrate skull is obliterated. In the turtle, for example (Fig. 460), the doubleness of the skull is still evident. The inner part immediately around the brain and the large roof-like outer region, it should be added, do not correspond strictly to the "double skull" of lower vertebrates just described. The outer skull of the turtle is large in order to provide for the adequate attachment of the head muscles, rather than to accommodate the brain, which is disappointingly small. In fact the size of the visible skull is not always a true guide to the size of the brain within, since between the small inner skull that fits close around the brain, and the vaulted outer skull, there is a large, vacant, unused space like an unfinished attic in a house.

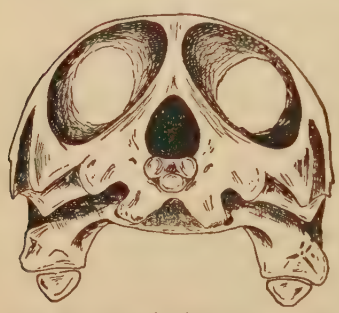


FIG. 460.—Back view of a turtle's skull, showing the false roof and large air spaces over the part of the skull that immediately covers the brain. (The *foramen magnum* is shown in black.)

I. BONE-COMPLEX STAGE

The final stage in the embryonic development as well as in the evolution of the human cranium, is brought about by the fusion of neighboring bones into complexes that thereafter pass for single bones. Thus, the *sphenoid* bone in adult man is a combination of at least ten embryonic bones, the *basi-* and *presphenoids*, which are represented throughout life in certain vertebrates as single bones, although arising respectively from two centers of ossification, and the paired *orbitosphenoids*, *alisphenoids*, *pterygoids*, and *median lamellæ*.

Since a light, strong brain case is necessary for purposes of flight, the process of the formation of bone complexes in the avian skull has gone to such an extreme that most of the sutures become obliterated in adult life, so that a bird's cranium presents almost the appearance of a single bone.

In the human skull, as previously intimated, all the evolutionary stages described in the preceding paragraphs, are not repeated. The outer, or investing skull, for instance, begins its rapid development before the inner cartilaginous skull is completed. Conse-

quently, the up-growth and roofing-over stages are omitted, being rendered unnecessary in the replacing of cartilaginous material. There remain, nevertheless, unmistakable evidences of the dual origin of the outer and inner skull even in man.

2. The Splanchnocranium

The description of the skull thus far given applies solely to the *neurocranium* which invests the end of the neural tube, that is, the brain. The other morphological half of the skull, namely, the *splanchnocranium*, surrounds the anterior end of the digestive tube primitively in the form of a series of cartilaginous arches.

Among the lower water-dwelling vertebrates the splanchnocranium is relatively large, while higher up in the evolutionary scale it becomes more and more reduced. The converse is true of the neurocranium which increases in importance with the increasing size of the brain.

The primitive arrangement of the splanchnocranium may best be understood by reference to the skull of the dogfish (Fig. 227), where the distinction between the neurocranium and the splanchnocranium is still clearly defined. Here there are present seven cartilaginous arches arranged around the anterior part of the digestive tube, one behind the other, like horseshoes with the open ends up. Each arch is composed of a number of separate elements that articulate in zigzag fashion so that the arch as a whole may be enlarged or contracted to some extent as adaptively needed.

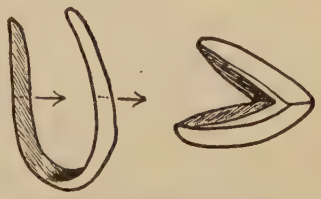


Fig. 461. — Diagram to show how the primitive upper and lower jaws form from a horseshoe-shaped cartilaginous arch.

The first, or *mandibular arch*, which is the most anterior one, is made up of only four elements, that bend back to form a junction on either side, and thus become the jaws, shown diagrammatically in Fig. 461.

The second, or *hyoid arch*, emancipated like the mandibular arch from bearing gills, is largely a suspensory apparatus, furnishing the only points of articulation between the neurocranium and the splanchnocranium (Fig. 277).

The five posterior arches are *gill arches* that in the manner of ribs extend around, protecting the anterior end of the digestive

tube (Fig. 462). Between these pairs of arches are gill slits, which allow water entering the mouth to pass out on either side after bathing the vascular gills that hang suspended from the arches. The gill arches diminish in size posteriorly and also numerically in bony fishes, the loss always coming at the posterior end of the series.

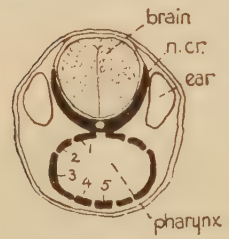


Fig. 462. — Cross section diagram through the primordial neuro- and splanchnocranium. *1*, pharyngobranchial; *2*, epibranchial; *3*, ceratobranchial; *4*, hypobranchial; *5*, basibranchial; *n.cr.*, neurocranium. (After Wiedersheim.)

In the evolution of the vertebrates, as the need for respiratory gills gives way with the rise of lungs, the gill arches become relegated to what may be called the anatomical scrap heap. There still persist embryonic traces of the primitive splanchnocranium in the form of three pairs of temporary and non-functional gill arches that later vanish. Thus is the legendary history of remote ancestors retold even in the human embryo. The gill arches are not entirely lost, however, for certain parts of the mature skeleton are directly derived from the primitive splanchnocranium inherited from ancestral water-dwellers. Nowhere is the thrift and resourcefulness of Nature better exemplified than in the disposal of the parts of the splanchnocranium after they have outlasted their original use, owing to the emergence of vertebrates from life in water to land. What becomes of the different elements that make up the splanchnic part of the primitive skull is represented graphically in Figs. 463 and 464, where the theoretical extent and position of the original arches are drawn as a background for the relics that persist. The same is also indicated below in tabular form.

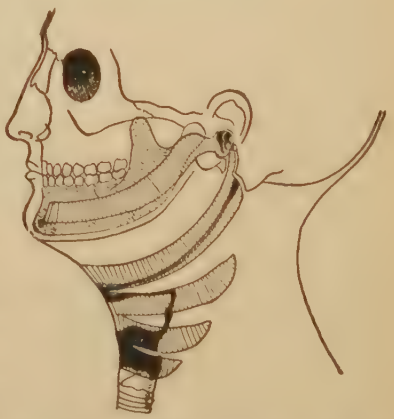


Fig. 463.—Diagram to show the fate of the ancestral splanchnic arches in man. (The arches are represented by the areas shaded with parallel lines, and the parts of them which persist in adult man are shown in black. See Table on page 517.) (After Wiedersheim.)

FATE OF THE SPLANCHNOCRANIUM

NUMBER OF ARCH	ELASMOBRANCHS	OTHER FISHES	AMPHIBIANS	REPTILES AND BIRDS	MAMMALS
1	Upper and Lower Jaw	Pterygoquadrate and Meckel's Cartilage			Incus Malleus Meckel's Cartilage
2	Hyoid Arch	Hyomandibular Symplectic Hyoid	Columella Hyoid Apparatus	Stapes Hyoid Apparatus	Stapes Styloid Process External Ear Cartilage Hyoid Apparatus
3	First Gill Arch		Hyoid Apparatus		
4	Second Gill Arch		Hyoid Apparatus Missing		Thyreoid Cartilage
5	Third Gill Arch		Missing		Thyreoid Cartilage
6	Fourth Gill Arch		Missing		Epiglottis
7	Fifth Gill Arch		Tracheal Cartilages		

It will be seen that the embryonic skeletal material which originally had to do with respiration and the support and protection of the anterior end of the digestive tube, has now, by a complicated series of makeshifts, assumed very diverse functions, such as the support of the vocal apparatus and the muscular tongue, or the transmission of sound waves to the inner ear.

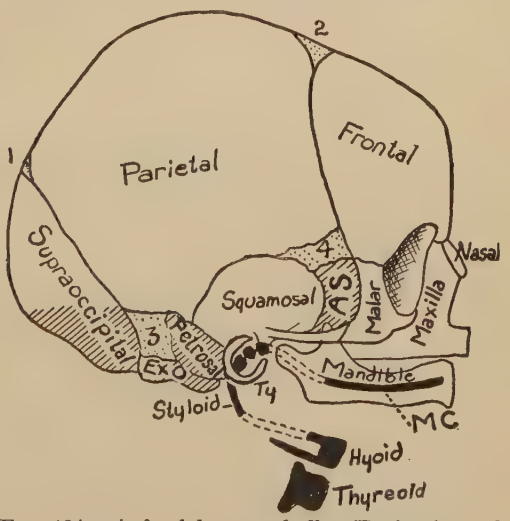


FIG. 464.—A fetal human skull. (Derivatives of the splanchnocranium are shown in black; fontanelles, dotted; investing bones unshaded; replacing bones shaded.) *Ty*, tympanic ring; *Ex.O*, exoccipital; *AS*, alisphenoid; *MC*, Meckel's cartilage; *1*, occipital fontanelle; *2*, parietal fontanelle; *3*, mastoidal fontanelle; *4*, sphenoidal fontanelle. (After McMurrich.)

3. Vicissitudes of the Vertebrate Jaws

In such fishes as the dogfish the first splanchnic arch, as already seen, serves the purpose of jaws (Fig. 461). Its upper

elements on either side, which form the upper jaw, are termed the *pterygoquadrates*, while the lower half, constituting the lower jaw, are named *Meckel's cartilages* (Figs. 277 and 464).

The cartilaginous splanchnocranium, which follows the same sequence of development as the neurocranium, becomes overlaid in part by an outer bony splanchnocranium, formed directly of platelike elements that arise externally as scales do (*investing bones*), rather than as patterns of cartilage later copied into bony tissue (*replacing bones*). In this way Meckel's cartilage in the primitive lower jaw becomes encased by a number of investing bones. Some of these bones eventually bear teeth, which take over the function that was first performed by Meckel's cartilage. In the lower jaw of the alligator these investing bones are still distinct, being separated from each other by definite sutures (Fig. 465). In man they not only fuse together on either side, but the two sides

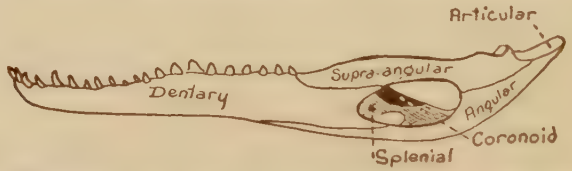


FIG. 465.—The lower jaw of an alligator, showing its six component bones. (After Schimkewitsch.)

also unite into a single bone, called the *mandible*. As the investing bones increase, Meckel's cartilage decreases until, in adult life, it entirely disappears, with the exception of its proximal articular end, which moves up into the neurocranium to be transformed into the *malleus*, one of the tiny ear bones in the middle-ear chamber. Thus the joints at the angles of the jaws of elasmobranch fishes, are gradually transferred to the inside of the ear in the higher forms.

There are at least five ways in which the lower jaw may be suspended from the neurocranium, namely, hyostylic, amphistylic, two autostylic methods, and craniostylic.

The *hyostylic* method of suspension as found among elasmobranchs (Fig. 466, A), is that in which the only skeletal articulations of the lower jaw with the neurocranium are between the hyoid arch on either side and the base of the neurocranium. Although ligaments attach the pterygoquadrate, or upper jaw, and Meckel's cartilage, or the lower jaw, to the hyoid arch, and thus

indirectly to the neurocranium, there are no direct articulations between the jaws and the cranium.

Amphistylic suspension, that is, where both the pterygoquadrate and the hyoid arch make direct articulation with the neurocranium, occurs in the primitive shark, *Notidanus* (Fig. 466, B), and also in *Lepisosteus* and *Amia* among ganoids.

The third method, *autostylic*, is exemplified by the elephant fishes, *Holocephali* (Fig. 466, C). Here the pterygoquadrate is

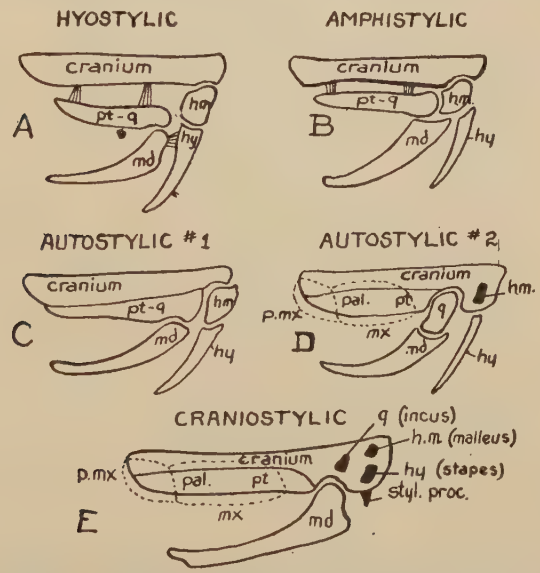


FIG. 466.—Diagrams of different methods of suspension for the lower jaw. *A*, hyostylic (elasmobranchs); *B*, amphistylic (*Notidanus*, a primitive shark); *C*, autostylic #1 (holocephalans); *D*, autostylic #2 (many dipnoans, ganoids, teleosts, amphibians, reptiles, and birds); *E*, craniostylic (mammals). *h.m.*, hyomandibular; *hy*, hyoid; *md*, mandible; *mx*, maxilla; *pal*, palatine; *pt.q*, pterygoquadrate; *p.mx*, premaxillary; *q*, quadrate; *styl.proc.*, styloid process.

anchylosed to the neurocranium directly, the hyoid being disconnected, thus making the suspension of the lower jaw and the other parts of the splanchnocranium entirely dependent upon the mediation of the pterygoquadrate.

The fourth method, also *autostylic* in type, is characteristic of dipnoans, amphibians, reptiles, and birds. It differs in one important particular from the preceding method since the pterygoquadrate becomes two distinct bones, the *pterygoid* and the *quadrate*,

with the quadrate alone remaining the intermediary between the lower jaw and the cranium (Fig. 466, D).

Lastly, in mammals the quadrate undergoes a profound change, becoming the *incus bone* of the middle ear, which leaves the lower

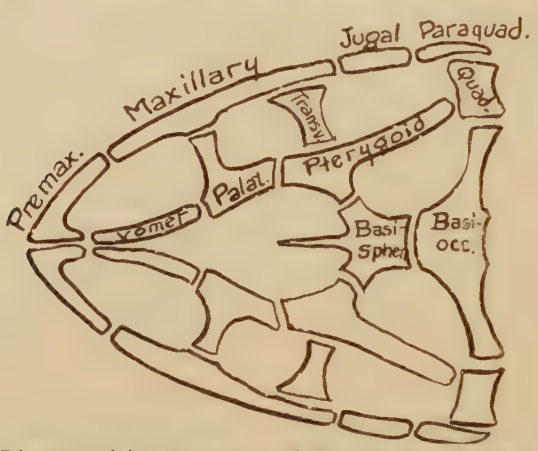


FIG. 467.—Diagram of jaw apparatus of Sauropsida, ventral view. (After Bütschli.)

jaw articulating directly with the cranium according to the *craniostylic* method of suspension (Fig. 466, E).

The evolutionary history of the upper jaw is the same in principle as that of the lower jaw, but somewhat more complex in detail.

FIG. 468.—Diagrammatic cross section through the jaws, looking down the throat of *A*, a dogfish; *B*, a bony fish; and *C*, a mammal, to show the evolution of the mammalian hard palate from *pq*, the upper jaw of elasmobranch fishes. *pq*, pterygoquadrate; *mc*, Meckel's cartilage; *mx*, maxillary; *d*, dentary; *c*, coronary; *p*, palatine; *md*, mandibular.

On the exterior surface of the pterygoquadrate cartilage of the lower vertebrates, secondary investing bones form on either side, the *maxillary* and *premaxillary*, that bear the teeth and take

over the function of the upper jaw. Meanwhile, the pterygoquadrate cartilage ossifies into two bones, the *pterygoid* and the *quadrate*, which, being relieved from the original work of the jaw, now become adapted to new uses, while an additional pair of investing bones, the *palatines*, develop in front of the pterygoids, making a chain of three bones on either side in place of the original pterygoquadrate (Fig. 467). The flattened palatines and pterygoids tip over from a vertical to a horizontal position and, widening out to meet their fellows on the other side, move in to form the "hard palate," or secondary roof of the mouth (Fig. 468). At the same time the quadrate, which still persists in its old position, serves as the point of articulation for the lower jaw in most vertebrates, except the craniostylic mammals, as noted above.

4. The Composite Vertebrate Skull

Although a great diversity appears in the general form of different vertebrate skulls, as well as in the arrangement of the separate elements taking part in their formation, it is possible to find a fundamental unity in the relationship of these elements. When such a fundamental plan is visualized, it becomes less difficult to interpret the topographical significance of the skull as well as to homologize its components which have departed from the typical condition in adaptation to the individual needs of different species.

It will be remembered that vertebrate skull bones are embryologically of two sorts, *replacing* and *investing*, indistinguishable from each other except when their development is known. The former are patterned in cartilage and become bone by replacement. The latter are ossified directly from subcutaneous connective tissue without any intermediate cartilaginous stage.

A composite vertebrate skull, which represents in a general way the skulls of all vertebrates, but is, therefore, necessarily inaccurate for any particular species, is diagrammatically represented in Fig. 469. The replacing bones form the principal part of the floor of the skull and the immediate surroundings of the sense capsules of the ears, eyes, and nostrils. Investing bones form the roof and the sides. Roughly the replacing bones are like a dish in which the brain reposes, while the investing bones form the cover of the dish. The key to Fig. 469 is given in the table on page 523, in which the skull bones are arranged in accordance with their

origin, and also in topographical groups. In Fig. 469 the replacing bones are stippled to distinguish them from the unstippled investing bones.

The poet Goethe, who was also a biologist far in advance of his time, conceived the skull to be a group of modified vertebræ, and on this assumption attempted to homologize the separate skull bones with the parts of a vertebra. While this idea is not generally accepted by comparative anatomists today, owing largely to

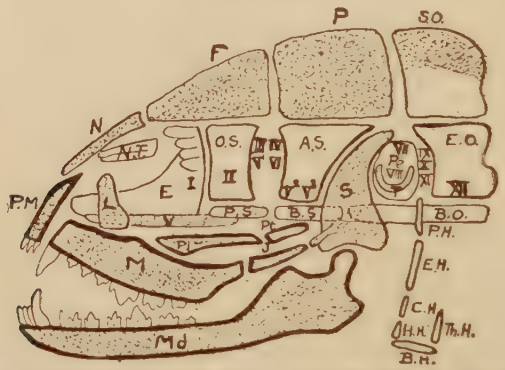


FIG. 469.—Composite mammalian skull. *Investing bones*, stippled; *replacing* bones in outline. *I–XII*, locations of the exits of cranial nerves. *A.S.*, alisphenoid; *B.O.*, basioccipital; *B.S.*, basisphenoid; *E*, ethmoid; *E.O.*, exoccipital; *F*, frontal; *J*, jugal; *L*, lacrimal; *M*, maxillary; *Md*, mandibular; *N*, nasal; *N.T.*, nasoturbinal; *O.S.* orbitosphenoid; *P*, parietal; *Pe*, petrosal; *P.M.*, premaxillary; *Pl*, palatine; *P.S.*, presphenoid; *Pt*, pterygoid; *S*, squamosal; *S.O.*, supraoccipital; *T*, tympanic; *V*, vomer; parts of hyoid, *P.H.*, pharyngohyal; *E.H.*, epihyal; *C.H.*, ceratohyal; *H.H.*, hypohyal; *B.H.*, basihyal; *Th.H.*, thyreohyal. (After Weber.)

objections from the side of embryology, it is convenient to use the "cranial vertebræ" of Goethe, together with their grouping in relation to the sense capsules, in classifying the bones of the neurocranium for purposes of description. (See Table on page 523.)

Starting at the posterior part of the skull, there are four bones arranged around the *foramen magnum*, through which the nerve cord is continuous with the brain. These are the ventrally located *basioccipital*, the two lateral *exoccipitals*, and a dorsal *supraoccipital*. According to Goethe the basioccipital corresponds to the centrum of the vertebra, the exoccipitals to the pedicels and side of the neural arch, and the supraoccipital to the keystone of the arch, or the neural spine.

A Catalogue of the Principal Skull Bones

Chart Number	Group	Replacing Bones	Investing Bones	Single or Double
1	1st arch	Basioccipital		S
2	of	Exoccipital		D
3	Goethe	Supraoccipital		S
4	2nd arch	Basisphenoid		S
5	of	Alisphenoid		D
6	Goethe		Parietal	S
7	3rd arch		Frontal	D
8	of	Presphenoid		S
9	Goethe	Orbitosphenoid		D
10	Nose	Mesethmoid		S
11	Region	Ectethmoid		D
12			Lacrimal	D
13			Nasal	D
14	Eye	Sclerotics		?
15	Region		Prefrontal	D
16			Postfrontal	D
17		Proötic		D
18		Opisthotic		D
19	Ear	Epiotic		D
20	Region	Sphenotic		D
21		Pterotic		D
22			Squamosal	D
23			Parasphenoid (Vomer)	S
24	Roof of		Vomer	D
25	Mouth		Palatine	D
26	Region	Pterygoid		D
27			Ecto-pterygoid	D
28	Upper	Quadrate		D
29	Jaw		Premaxillary	D
30	Region		Maxillary	D
31	Cheek		Jugal	D
32	Region		Quadratojugal	D
33		Articular		D
34	Lower	Mento-meckelian		D
35	Jaw		Dentary	D
36	Region		Splenial	D
37			Angular	D
38			Coronoid	D
39			Supra-angular	D
40	Hyoid	Hyomandibular		D
41	Region	Symplectic		D
42		Basihyal		S
43		Branchials		D
44	Gill		Opercular	D
45	Region		Preopercular	D
46			Subopercular	D
47			Interopercular	D

The supraoccipital is peculiar in that it is of compound origin. The lower part next to the foramen magnum is *replacing*, while that portion extending upward and encroaching upon the roof of the skull is *investing* in character. The exoccipitals are usually the part of the skull brought into articulation with the atlas, or first vertebra, and for that reason bear the *occipital condyles*, or articular surfaces.

The occipital condyles are absent in fishes, the head in these vertebrates not being movable upon the vertebral column. They are paired in amphibians and mammals, and in reptiles and birds they coalesce into a single one, in which not only the exoccipitals but also the basioccipital may take part. In crocodiles, however, the basioccipital alone bears the condyle.

Immediately in front of the occipital ring of bones is Goethe's "second arch," composed of the *basisphenoid*, two lateral *alisphenoids*, and the dorsally placed, investing *parietal*, which completes the arch.

Anterior to these four bones is Goethe's "third arch," which is made up of the *presphenoid* on the floor of the skull, with two lateral *orbitosphenoids* forming the sides, and the *frontal* bone on top. These twelve bones of Goethe's three imaginary cranial vertebræ, either separate or more or less fused together, form the foundation of every vertebrate skull above the elasmobranchs. Their identification aids greatly in determining the topographical relations of the remaining skull bones, which are largely grouped around the three pairs of sense capsules.

Anterior to the presphenoid, the cartilaginous floor of the skull expands into the ethmoid plate of the *Nose Region*, from which the median *mesethmoid*, and two lateral *ectethmoid* bones ossify. *Turbinal* bones may also eventually form from the latter. In addition the two dorsal *nasal* bones, and paired lateral *lacrimals*, from the fraternity of investing bones, belong to this group.

About the *Eye Region* of many vertebrates, particularly reptiles, in addition to the sphenoid, lacrimal, and various other bones mentioned under other groups which help to form the orbit, are the investing *prefrontals* and *postfrontals*. In the category of replacing bones also are sometimes found *sclerotic* bones, a ring of separate elements packed around inside the orbit, particularly in such birds as owls.

The *Ear Region* begins as a pair of cartilaginous capsules from

which three otic bones regularly ossify, the *proötic* in front, the *opisthotic* behind, and the *epiotic* above. Sometimes two additional otic bones, the *sphenotic* and *pterotic*, appear, notably in teleosts. The *squamosal*, or *paraquadrate*, is an investing bone that fuses with the otic bones in man to make the *temporal bone*, but which serves a varied apprenticeship in other vertebrates before this consummation, being probably homologous with the preopercular bone in the splanchnocranium of fishes, to be mentioned later.

The *Roof of the Mouth Region* including the floor of the cranium is characterized in fishes and amphibians by a pair of investing *vomer* bones and by the *parasphenoid*, also investing in character, which is so flattened out in urodeles that it almost covers the entire floor of the cranium. These bones, frequently bearing teeth, are missing in the amniotes, and their places are taken by the "hard palate," made up, as already described, of the paired *palatines* and *pterygoids* (Fig. 98), with a *median vomer* between them, that projects upwards, forming with the mesethmoid the partition separating the two nasal cavities. The median vomer of the higher vertebrates is probably not the homologue of the paired vomers of the fishes and amphibians. There is some probability that it is to be regarded as the transformed parasphenoid.

The bones of the splanchnocranium may likewise be arbitrarily classified into groups for purposes of description.

The *Upper Jaw Region.* This was originally represented by the pterygoquadrate that later became two distinct replacing bones, namely, the *pterygoid*, which goes to form a part of the base of the skull, and the *quadrate*, that serves as the middleman between the skull and the lower jaw in the autostylic dipnoans, amphibians, reptiles, and birds. In the craniostylic mammals, as already stated, the quadrate becomes metamorphosed into the incus bone, and is incorporated inside the otic capsule in the ear region. There is also included in the upper jaw region two paired investing bones bearing teeth, the *maxillary* and *premaxillary*, that assume the duties of the permanent jaw when the primary jaw migrates inward to form the roof of the mouth. Thus there is a succession of jaws in vertebrates, similar to the succession of hair, teeth, and nephridia.

The *Cheek Region.* Bridged by the *jugal* and *quadratojugal*, which fill the gap between the maxillary and the quadrate in

reptiles and birds, the cheek region constitutes the side of the face in mammals. In human anatomy the jugal bone is known as the *malar*, or cheek bone. There are no replacing bones in this region.

The *Lower Jaw Region.* The original Meckel's cartilage, which marks the lower jaw region, becomes proximally ossified into a bone called the *articular*, that plays upon the quadrate, while its distal end usually remains in cartilaginous form for a time, although it ossifies in certain Amphibia into the *mento-meckelian* bone. Around it investing bones form a sheath, after which the cartilage core eventually disappears except in the cases just indicated. The investing bones are the *dentary*, making the tooth-bearing edge around the distal end; the *supra-angular*, along the upper edge of the proximal end, posterior to the dentary, the *angular*, along the ventral edge and forming the posterior angle of the jaw; and the *splenial* and *coronoid* on the inner surface of the jaw, the former being anterior to the latter.

The *Hyoid Region.* In this region are included the hyoid arch and its derivatives. The original arch breaks up into a *hyomandibular*, *symplectic*, and *ceratohyal* on either side, joined by a median *basihyal*, which becomes the skeletal foundation of the tongue in fishes. The hyomandibular in the Anura migrates up into the auditory region of the cranium and becomes the *columella*, a rodlike bone resting against the tympanum of the ear, that assists in the amplification of sound waves. In mammals the columella forms the *stapes*, the innermost of the chain of middle ear bones.

The *Gill Region.* This region has both replacing and investing bones. The replacing bones are represented by the important *branchial arches*, which break up into *pharyngo-*, *epi-*, *cerato-*, *hypo-*, and *basibranchial* elements in fishes (Fig. 462), but which lose their importance with the passing of gill breathing, and remain only as fragmentary relics in the form of tracheal cartilages in higher vertebrates.

The investing bones which appear over the outside of the branchial arches in the teleost fishes, consist of four thin flat bones on either side, the *opercular*, *preopercular*, *subopercular*, and *interopercular*, forming the flap beneath which the gills find protection. It is possible that the preopercular bone of fishes

is homologous with the squamosal bone of higher forms, but with this exception the other opercular bones entirely disappear in land vertebrates.

5. Comparative Anatomy of the Skull

A. Cyclostomes

The skull of cyclostomes (Fig. 470), is not only very primitive, but it is also quite aberrant from that of other vertebrates. In the embryonic *"Ammocœtes"* stage of *Petromyzon*, the paracordalia and trabeculæ of the brain case floor are evident and normal, as well as the otic capsules that surround the ears, but a cartilaginous envelope does not entirely surround the brain, as

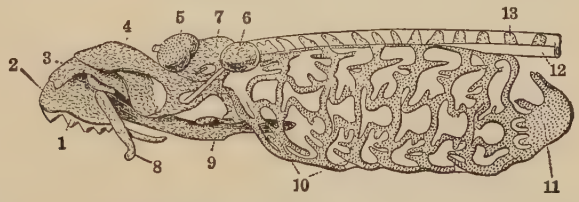


Fig. 470.—Lateral view of skull of *Petromyzon*. *1*, horny teeth; *2*, annular cartilage; *3*, anterior labial cartilage; *4*, posterior labial cartilage; *5*, nasal capsule; *6*, auditory capsule; *7*, dorsal portion of trabeculæ; *8*, lateral distal labial cartilage; *9*, lingual cartilage; *10*, branchial basket; *11*, cartilaginous cup supporting pericardium; *12*, sheath of notochord; *13*, anterior neural arches, fused together. (From Shipley and MacBride, after Parker.)

the roof of the brain case is completed in fibrous connective tissue, while the absence of jaws changes entirely the character of the anterior part of the skull.

The skeleton of the large tongue may possibly be homologous with the lower jaw of fishes. At any rate, it bears rasping epidermal teeth and is bilateral in origin like the lower jaw. The cartilaginous elements anterior to it, which support the jawless mouth, seem to be peculiar to cyclostomes, and are adaptations necessary on account of the suctorial and parasitic habits of these animals.

The posterior part of the cranium, which ends abruptly with the otic capsules, is consequently without any true occipital region. Since in higher vertebrates this region is to be regarded as a derivative of the anterior vertebræ, as the relation of the posterior cranial nerves indicates, it could hardly be expected to be developed in animals whose skeletal axis has not emerged from the notochordal stage.

Finally, the skeletal support for the gills is a continuous grillwork of cartilage, more external in position than the splanchnocranium of other fishes and difficult to homologize with it.

B. Elasmobranchs

The typical cartilaginous skull of elasmobranchs furnishes a morphological point of departure for the skulls of all other vertebrates (Figs. 227 and 457). The neurocranium is a continuous protective brain case, the result of fusion of embryonic cartilaginous elements already described; and the splanchnocranium is present in its most perfected form, being nowhere fused or incorporated with the neurocranium.

The first arch of the splanchnocranium serves as both upper and lower jaws and is abundantly supplied with teeth.

Perhaps the feature most peculiar to the elasmobranch skull, and least copied by subsequent forms, is the development of snout-formation, by means of *rostral cartilages*, which project anteriorly, thus making the mouth ventral in position.

C. Cartilaginous Ganoids

The transition from a single cartilaginous skull to a double skull is found in this group, which serves as a "connecting link" in this respect between the lower fishes and higher vertebrates. While an inner cartilaginous capsule is retained unossified around the brain, there is added to the outside of it a bony skull of many parts, derived from dermal scales (Fig. 458). All the bones in the skulls of cartilaginous ganoids are of the investing type, but they are very numerous and of doubtful individual homology with the investing bones of the skulls of higher forms.

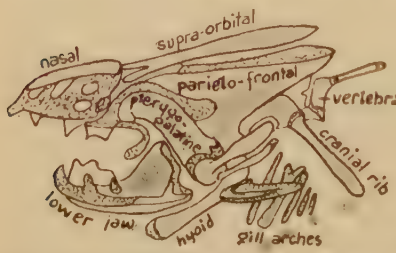


Fig. 471.—Skull of a lungfish, *Lepidosiren*. Cartilage stippled. (From Bütschli, after Bridge.)

The number of elements in the splanchnocranium is reduced somewhat as compared with the elasmobranchs.

D. Bony Ganoids

The skulls of bony ganoids (Fig. 471) have two sets of bone, investing on the outside and replacing on the inside, the latter formed from the cartilaginous brain case. Much cartilage remains, however, after the replacing bones appear.

E. Lungfishes

The Dipnoi generally are intermediate between bony ganoids and teleosts on the one hand, and Amphibia on the other. The inside cartilaginous cranium furnishes only a few replacing bones, notably those of the occipital region, and investing bones are also reduced in number by fusion and otherwise, thus approaching the simplicity of structure that characterizes the amphibian skull. For example, a single *frontoparietal* bone takes the place of the two pairs of bones, *frontals* and *parietals*, ordinarily found on the roof of the skull.

In *Protopterus* and *Lepidosiren* occurs a pair of unique replacing bones, the "cranial ribs," extending from the base of the skull backward and downward across the shoulder girdle.

F. Teleosts

Bony fishes exhibit a great variety of skulls, all referable more or less directly to the type characteristic of bony ganoids. In the lower teleosts considerable cartilage persists unossified, but in most cases the name "teleost" (*tele*, entire; *ost*, bone) is justified (Fig. 472). No other vertebrates have as many replacing bones as teleosts.

In the splanchnocranium a secondary jaw is evolved with premaxillary and maxillary elements bearing the teeth, while the pterygoid, from the primary pterygoquadrate jaw, breaks up into three separate elements, the *ento-*, *meso-*, and *metapterygoid*, which span the mouth cavity like slanting girders, caught in the very act of changing from vertical jaws into a horizontal "hard palate."

The *symplectics*, which are found only in teleosts and two ganoids, *Acipenser* and *Spatularia*, appear distal to the hyoid bones as a part of the hyoid arch.

G. Stegocephalans

The problematical extinct Stegocephali, some of which had skulls over three feet in length, show a large number of investing bones, making an extensive roof over a cranium of very small capacity. For the most part these bones fit closely together, allowing only for restricted orbital and nasal pits, suggesting the skull of the bony ganoids rather than that of an amphibian type. Between the parietal plates on the top of the skull is an *interparietal foramen*, the window out of which probably a third parietal eye looked upward. There was abundant reason for these lowly monsters to look upward, at least in an evolutionary sense.

H. Amphibians

Amphibians are characterized by much less cartilage in the skull and fewer bones than are the bony fishes. It is quite probable that they represent a separate divergent evolutionary line, distinct

Fig. 472.—Disarticulated bones of a teleost skull, *Gadus*. (After W. K. Parker.)

from that of the teleosts, although both may be referred to a common origin in the elasmobranchs.

The cranium itself that houses the brain is somewhat tubular and elongated, extending far anterior between the eyes without

any interorbital septum. The conspicuous width of the skull is largely due to outrigger bones which form the upper jaw and connect with the widened ethmoid and auditory regions. Of the few replacing bones, the exoccipitals, bearing the two condyles, and the proötics, which make up the major part of the otic capsule, are the most constant. There are no basi-, or supraoccipitals, but the place of the latter is taken by a band of connective tissue, or a narrow cartilage, the *tectum synoticum*, which joins the two otic capsules together. There is also a round opening on the external face of the capsule, the *fenestra vestibuli*, which is filled in by a *stapes plate*, or *operculum*, derived from the hyoid arch. In the Anura a slender *columella* bone is contributed to the ear apparatus by the hyoid arch, instead of a stapes plate.

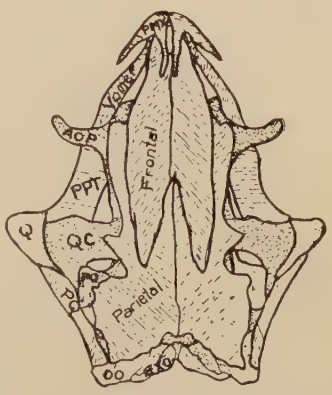


FIG. 473.—Dorsal view of skull of *Necturus*, with nasal capsules removed. *AOP*, ante-orbital process; *EXO*, exoccipital; *OO*, opisthotic; *PMX*, premaxillary; *PO*, proötic; *PQ*, paraquadrate; *PPT*, palato-pterygoid; *Q*, quadrate; *QC*, quadrate cartilage. (After Wilder.)

The quadrate, on which the lower jaw articulates, becomes united with the cranium, and the lower jaw itself never involves more than five bones, including the two replacing bones, *articular* and *mento-meckelian*, formed from Meckel's cartilage.

Investing bones of the amphibian skull are reduced in number and are separated from the corium, thus occupying a deeper position than the corresponding investing bones of fishes, although they are still sufficiently distinct from underlying replacing bones to be easily separable.

In urodeles there is a greater parsimony of the inside cartilaginous skull than in anurans, since the primitive trabeculæ never meet and fuse, leaving this region of the skull without a cartilaginous floor, as in the adult *Necturus*, (Fig. 473). The quadrate and pterygoid are continuous, the quadratojugal fuses with the squamosal, and the paired vomers and palatines join, but unlike the neurocranium of the anurans, the parietals and frontals remain distinct. The parasphenoid in urodeles is a large flat investing bone, some-

times provided with teeth and covering nearly the entire floor of the skull, whereas in the Anura it is reduced to a peculiar T-shaped structure, with the shaft pointing anteriorly (Fig. 474).

Little of the original cartilage remains in the skull of the legless cæcilians (Apoda), but there is more fusion of the investing bones than in urodeles. The parasphenoid and the basisphenoid, for example, fuse into a common basal plate, the *os basale*.

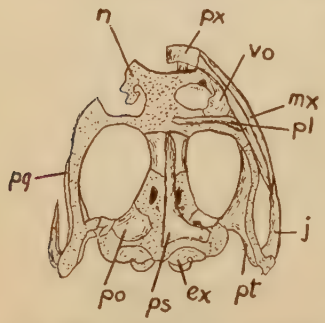


FIG. 474.—Ventral view of frog's skull. The investing bones have been removed from one side, and the primordial cartilaginous skeleton is dotted. *n*, nasal cartilage; *pq*, palatoquadrate; *j*, jugal; *mx*, maxillary; *px*, premaxillary; *pt*, pterygoid; *vo*, vomer; *pl*, palatine; *ps*, parasphenoid; *po*, proötic; *ex* exoccipital. (After Ecker.)

I. Reptiles

Cartilage largely disappears from the reptilian skull, persisting in *Sphenodon* and in lizards to a greater extent than in other modern reptiles. Investing bones are more numerous than in amphibians, while replacing bones are many and usually independent or unfused. The occipital bones ossify, and there is only a single occipital condyle located on the basioccipital in crocodiles and with components from both exoccipitals and basioccipitals in other reptiles. Except in snakes an *interorbital septum* separates the two orbits of the eyes and consequently the brain does not extend as far anteriorly as in amphibians. Between the pterygoid and maxillary a *transverse* or *ectopterygoid* bone is present in most reptiles except the chelonians.

In lizards the exoccipitals and opisthotics fuse together to form the *oto-occipitals*, the parasphenoid is reduced in size and anchylosed with the basisphenoid, and a *parietal foramen*, for a possible third eye, as in *Sphenodon*, is common. The premaxillaries, which are usually united in adult reptiles, are double embryologically, and the same is true of the parietals. Meckel's cartilage is persistent although surrounded by a full complement of six investing bones.

In chelonians a false roof to the skull, formed by expanded postfrontals, parietals, and squamosals, reminds one of the Stegocephali, while the supraoccipital is often prolonged backward into

a conspicuous spine. The entire chelonian skull is deceptively large when the actual size of the brain within is considered. A single *median vomer* and the parietals, which remain unfused, are present, but several bones that might be expected such as the nasals, orbito- and alisphenoids, ectopterygoid, and lacrimals, are absent.

The jaws of snakes are a distinctive feature, since they are capable of great distension, enabling these animals to swallow their relatively large prey whole. To accomplish this feat the palatines are movably articulated with the pterygoids, which do not form a rigid hard palate, while the two parts of the lower jaw are not only loosely joined to the cranium on either side by the movable quadrates but are also anteriorly united together by an elastic ligament that permits their separation to a considerable extent.

In crocodiles and lizards the two parts of the lower jaw are joined more firmly in front by sutures, and in turtles they are fused into one solid *mandible*. In crocodiles the parietals and frontals each fuse into single bones, but in snakes only the parietals fuse.

The formation of an extensive hard palate in crocodiles and alligators, in which the maxillæ, palatines, and pterygoids all take part, causes the posterior opening of the choana on either side to be pushed so far back down the throat that these animals are able to drown their prey without drowning themselves. This is accomplished by the aid of a curtain-like *velum* that shuts off the posterior openings of the nostrils from the surrounding water, enabling the reptile to breathe through the choanæ with the tip of the nose out of the water, while the capacious mouth cavity is kept submerged until the struggling prey within, which is held fast by the conical teeth, is dead (Fig. 347).

J. Birds

In birds the most characteristic feature of the skull, like that of the entire skeleton, is the elimination of every bit of bone that can be spared (Fig. 475). Compared with reptiles, a typical avian skull most resembles that of lizards, yet with some striking differences. Although the cranium is much rounder and roomier, the relatively enormous size of the eyes together with the well developed interorbital septum, tend to restrict the brain to the posterior part, while the ear capsules are more deeply embedded.

Although many typical bones, both replacing and investing, are present that are distinguishable in the embryo, in the adult they become welded together by the early closure of the sutures into an almost continuous capsule of bone, which is remarkably strong and protective in spite of its lightness and the paucity of bony material.

The zygomatic arch is confined to a slender bar; the postfrontals disappear, while the palatines and pterygoids are so narrowed that they fail to join into a hard palate. The lightness of the skull is furthermore enhanced by the pneumaticity of the bones, characteristic of the entire skeleton, as well as by the substitution of a horny beak in place of heavy teeth in the jaws. Only in the interorbital septum and the restricted ethmoidal region, does cartilage persist.

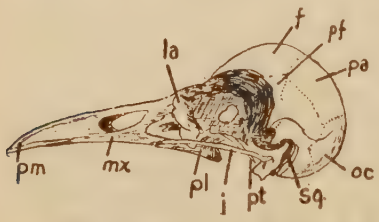


FIG. 475.—Lateral view of the skull of a crow. *pm*, premaxillary; *la*, lacrimal; *f*, frontal; *pf*, prefrontal; *pa*, parietal; *oc*, occipital; *sq*, squamosal; *pt*, pterygoid; *j*, jugal; *pl*, palatine; *mx*, maxillary. (After Haller.)

Remains of the investing parasphenoid fuse with the replacing basisphenoid to form a peculiar forward-projecting *sphenoidal rostrum* along the floor of the cranium. The single occipital condyle on the basioccipital region is similar to that in reptiles, but has rotated forward, along with the foramen magnum, until these two landmarks are at the base of the skull, instead of on the posterior aspect of it. This change, which is associated with the semi-erect attitude of birds, modifies the way in which the skull is carried by the vertebral column. The quadrate articulates freely with the skull, suspending the lower jaw. Parrots have a true joint between the upper jaw and the skull, and so can lift the upper jaw without at the same time carrying the cranium with it, an unusual performance for a vertebrate (Fig. 476).

FIG. 476.—Diagram to show the movable upper jaw of a parrot. (After Boaz.)

The hyoid apparatus of woodpeckers exhibits a peculiar modification also, in connection with the withdrawal of the extended tongue, as previously described.

K. Mammals

The skull bones of the primitive monotremes are highly specialized on account of their beaklike mouth parts, and the early fusion of the bones which obliterates the outlines of the component parts. They, therefore, present problems that make them of limited use in working out the homologies of other mammalian skull bones.

In general it may be said of the mammalian skull that the splanchnocranium becomes more completely incorporated with the neurocranium than in the skull of any other class of vertebrates. The orbits of the eyes are close together, separated by a thin septum without any intervening part of the brain between them. It is difficult to imagine how monstrous a human skull would be if, like that of the bird, each orbit were as capacious as the entire cranial cavity.

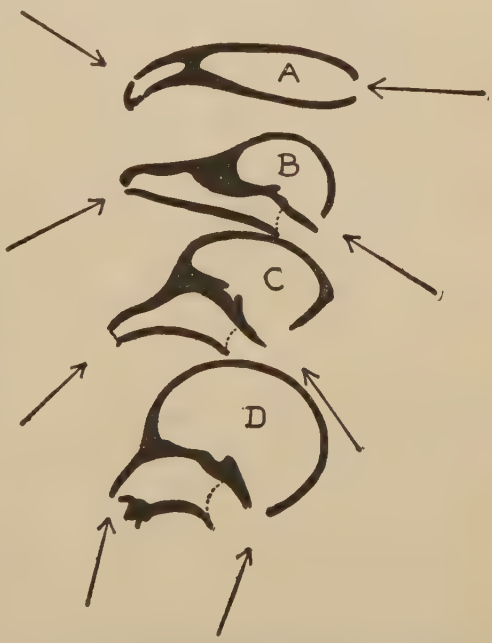


Fig. 477.—Sagittal diagrams through the skulls of, *A*, a salamander; *B*, deer; *C*, baboon; and *D*, man. (The arrows indicate an evolutionary change in the relation of the external nose-opening and the *foramen magnum*.) (Modified from Wiedersheim.)

With the process of cranial expansion to accommodate the increasing size of the brain, there is a shortening of the jaws, and a retreat of the face bones, which consequently become more and more overshadowed by the upward-bulging cranium, until, in primates at least, they are ventral to the cranium rather than anterior to it in position.

This evolutionary tendency is made clear when one compares the *facial angle* (Huxley) of a deer with that of man (Fig. 477), an angle obtained by drawing two imaginary lines, the first from

the foramen magnum to the point where the presphenoid and ethmoid join medially, the second from the presphenoid-ethmoidal junction to the point of union between the two premaxillaries at the tip of the lower jaw. In monotremes and other primitive mammals this angle is practically 180°, while in man it may be even less than 90°.

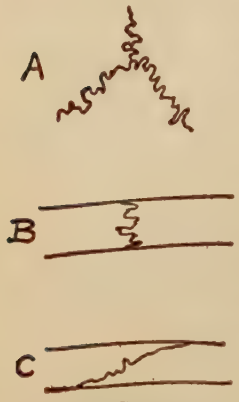


FIG. 478.—Sutures. *A*, surface view; *B*, cross section of interlocking suture; *C*, cross section of squamosal suture.

Although there is considerable fusion of bones in the mammalian skull, the sutures usually remain quite distinct, except in old age when they are apt to become obliterated. The sutures are of the zigzag type, formed by the dovetailing of the bones together edge to edge in an interlocking joint almost as firmly as solid bone (Fig. 478), or they may result from a shingling, or beveling, of one bone over another, as in the *squamosal suture* of the human skull.

When skull bones develop, they grow out from centers of ossification, like spreading ripples from a pebble thrown into a quiet pond, with the result that when the advancing edges of three or more enlarging bones meet, a small uncovered area is temporarily caught between them where they come together. Such an area is called a *fontanelle*, so named by some imaginative father of anatomy because the throbbing of the blood vessels of the human infant's brain, which is visible through these openings, suggests a "little fountain." In man at least six fontanelles are present at birth (Fig. 479): first, a large diamond-shaped *parietal fontanelle* on top of the head between the frontal and the two parietal bones, which does not close until about the end of the second year; second, the *occipital fontanelle*, triangular in shape and lying between the occipital and parietal bones, that closes at the end of a few months; third, a

FIG. 479.—The skull of a new-born infant, showing the location of the fontanelles. *O*, occipital; *P*, parietal; *M*, mastoidal; *S*, sphenoidal. (After Kollmann.)

pair of small *sphenoidal fontanelles*, which are formed on either side of the skull by the union of the frontal, parietal, temporal, and sphenoid bones; and fourth, the *mastoidal fontanelles*, likewise small and paired, that occupy the posterior space between the parietal, occipital, and temporal bones. In childbirth all these fontanelles are doubtless an adaptation of great practical value to large-headed man. As long as they persist, the separate bones of the cranium can move upon each other with considerable freedom even to the extent of temporarily shingling one over the other at the edges. Thus it is possible at birth, if the head has become somewhat misshapen in the process, to mold the cranium back into conventional contours without injury almost as if it were clay. Certain primitive races, like the Flathead Indians, have seized upon this possibility of molding the newly born infant's plastic skull in order to acquire an abnormal shape of the head which, if not an improvement upon nature, at least has the quality of lending distinction to its possessor.

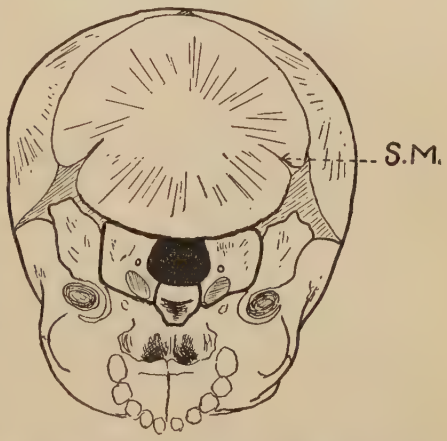


FIG. 480.—The base of an infant's skull before the fusion of the occipital bones. *S.M.*, suture of Medosa, which tends to separate the supraoccipital into an upper *investing*, and a lower *replacing* region.

The four embryonic and ancestral occipital bones of the mammalian skull eventually become joined into one *occipital bone* surrounding the foramen magnum, with the occipital condyles borne by the exoccipital elements although in some cases their ventral margins encroach somewhat upon the basioccipital. The presence of an embryonic notch, the *suture of Mendosa*, on either side of the supraoccipital component (Fig. 480), indicates the dual origin of the latter, the upper portion, which forms a part of the roof of the cranium, being *investing* in character, and the part below the suture of Mendosa, *replacing*, like the ex-, and basioccipitals.

In the sphenoid group of skull bones the alisphenoids fuse, forming on either side the upward-projecting wings of the basisphenoid, while the orbitosphenoids hold a similar relation to the presphenoid. Sometimes the suture between these two sphenoidal combinations remains open, but more often all the sphenoid bones fuse into a single bone of extremely irregular contour, the *sphenoid*, around which, as the main foundation of the cranium, the other bones are arranged. The basisphenoid in some cases may fuse with the basioccipital behind, and likewise the presphenoid may fuse with the ethmoid in front.

On the dorsal side of the basisphenoid, a hollowed-out place, the *sella turcica*, in which the hypophysis of the brain is seated, represents the embryonic junction-point of the trabeculæ with the parachordalia in forming the primitive floor of the cranium. Similarly, on the dorsal side of the sphenoid is a hollow in which lies the chiasma of the optic nerves. Both ali- and orbitosphenoidal wings take part in forming the wall of the cranium and orbits, and the orbitosphenoids are penetrated by foramina for the exit of the optic nerves. Traces of the investing parasphenoid of lower vertebrates have been found in the embryo of *Echidna* by Gaupp and in marsupial embryos by Fuchs.

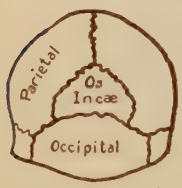


Fig. 481. — Diagram of the back side of a skull, showing the presence of the *Inca bone*. (After Wiedersheim.)

The generous roof of the mammalian cranium is covered by the paired *parietals* and *frontals*, with the parietals sometimes fused along the *sagittal suture* which joins them. In *Ornithorhynchus* a small parietal foramen also is found, that harks back to the third eye apparatus of reptiles.

An investing *interparietal bone*, either single or paired, appears with considerable constancy in several mammals. When it occurs in man it is known as the *os incæ*, for the reason that it has been very frequently found in the skulls of the aboriginal Incas of Peru (Fig. 481).

Among the Cetacea there is an abnormal shifting and compensation in the bones of the skull, with the parietal bones divorced from each other and shoved over to an extreme lateral position (Fig. 482), while the supraoccipital extends up between them as far as the frontals, making most of the roof of the skull.

Separating the frontals is the *metopic suture*, which is often

obliterated in postembryonic life, though occasionally persisting in man even after puberty. In many ungulates the frontal bones bear horns or antlers. Prefrontals and postfrontals are absent in mammals.

On account of the increasing size of the mammalian brain several of the cranial bones shift their position, among them the ear capsules, which come to occupy a place on the floor instead of the sides of the cranium. The ear capsules of mammals are formed by the fusion of the three paired otic bones into a single pair of *petrosal* bones that correspond to the ear capsules

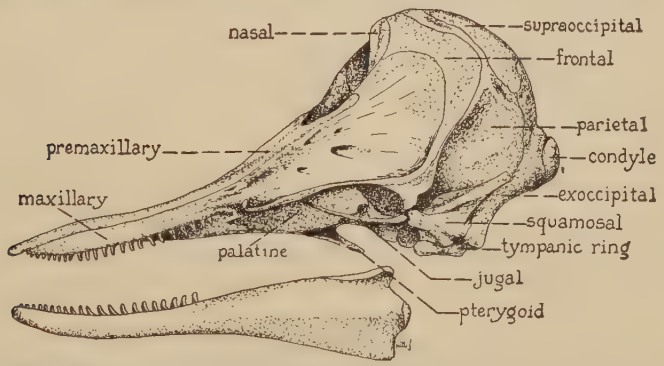


Fig. 482.—Skull of a dolphin, in which the bones of the cranium are much modified. (After Schimkewitsch.)

of reptiles, which have their origin largely from the proötics. Within the petrosals are embedded the ears each of which contains three pairs of ear bones, the *incus*, *malleus*, and *stapes*. The story of the circuitous derivation from splanchnocranial origins, of this triumvirate of the tiniest of bones, is as wonderful and extraordinary as anything in nature.

In a few mammals, man for instance, the squamosals become incorporated laterally with the petrosals, forming the *temporal bones*.

Included in the temporal complex also is a ringlike fragment on either side, the *tympanic bone*, across which the membranous ear drum is stretched (Fig. 483). This small bony element is probably the homolog of the quadratojugal of reptiles. The tympanic may enlarge into a thin-walled hemispherical structure, the *bulla ossea*, which is particularly prominent in rodents and carnivores.

The opisthotic region of the temporal complex becomes the *mastoid process* to which some of the jaw muscles are attached, while inserted into a socket just anterior to the mastoid process is the pointed *styloid process*, a remnant of the hyoid arch of the embryonic splanchnocranium.

Fig. 483.—Three stages in the development of the joint in the lower jaw of mammals, showing the inward migration of the quadrate, *Q*, and its transformation to the tympanic ring, *Ty*, resulting in the direct articulation of mandible, *M*, with squamosal, *S*. (After Gadow.)

The *ethmoid*, which ossifies slowly from its cartilaginous forerunner, is a delicate spongy bone that is placed between the orbits in front of the sphenoid (Fig. 484). In the embryo, the outer walls of the two nasal capsules ossify first, becoming the shell-like *ectethmoids*, and between these two curving plates the *mesethmoid* appears. All three of these embryonic elements finally unite to form the ethmoid bone, which straddles the nasal chamber. The mesethmoid forms further a thin upward projection, the *crista galli*, at the point where it fuses with the ectethmoid above, while below it forms a partition, the *perpendicular plate*, which divides the nasal chamber into right and left parts.

Fig. 484.—A vertical cut through the nasal region, showing the ethmoid and turbinal bones, in black. (After Tillaux.)

Projecting into the nasal chamber from the inner surface of each ectethmoid, are delicate scrolls of bone, very voluminous in carnivores but much reduced in man, called the *turbinals*. On either side of the crista galli in man, where the ectethmoid joins the mesethmoid horizontally, there is a bony area, the *cribriform plate*, which is perforated like the cover of a pepper-box for the passage of the brushlike olfactory nerves to the patches of sensory epithelium in the nasal chambers. This multiplicity of foramina for the olfactory nerves is peculiarly mammalian. In *Ornithorhynchus* there is only a single pair of olfactory foramina, while the Cetacea, which

have apparently lost the sense of smell, have no cribriform perforations.

The ethmoid takes part too in the formation of the cranial capsule in many mammals, a condition more amphibian in character than reptilian.

The *nasals*, which sometimes fuse, roof over the nostrils and play a prominent part in snout formation.

Between the nasals and the outer margin of the frontals, are the *lacrimals*. These are always on the inner side of the orbit in mammals and are usually pierced by the foramina for the lacrimal ducts, except in cetaceans, sirenians, and elephants. The lacrimals may be homologous with the prefrontals of reptiles, which they more resemble than the "lacrimals" of the latter.

Premaxillaries are wanting in bats and certain edentates, but are usually present in other mammals. In the Cetacea they are excessively developed, so much so that they encroach even upon the roof of the cranium.

The *maxillæ* not only bear teeth and serve as upper jaws, but they also extend inward, forming a part of the hard palate. In man the maxillæ are hollowed out on either side by a large irregular sinus, called the *antrum of Highmore*.

To the posterior part of the *palatines* that also help to make the hard palate, are attached the *pterygoids*, reduced in size to mere processes in the mammalian skull.

The *jugals*, which are called the *malars* in human anatomy, form *zygomatic arches*, or "cheek bones," by connecting with processes from the squamosals posteriorly and the maxillaries anteriorly.

Set on edge between the sphenoid and the mesethmoid and forming the lower part of the nasal septum, is a thin "ploughshare bone," the single *median vomer* of mammals, which is not homologous with the paired vomers of lower vertebrates.

The *mandible*, or lower jaw, is craniostylic, articulating at the *glenoid fossa* directly to the immovable squamosal element of the temporal complex. In bats, perissodactyls, and primates, the mandibles of the two sides are fused into one solid piece.

All that is left to tell the tale of the splanchnic arches that formed so conspicuous and independent a part of the elasmobranch skull, are *Meckel's cartilage* of the embryonic mandibular arch, and remains of the hyoid arch in the form of the *styloid*

process of the temporal complex, the *hyoid bone* of the larynx, the *thyreoid cartilage*, and some of the cartilaginous *tracheal rings* (Fig. 463).

V. THE LOCOMOTOR SKELETON

1. The Necessity for Animal Locomotion

Attention has already been called in a general way to the necessity for locomotion among animals as contrasted with plants. The chemical elements common to all protoplasm, and therefore the

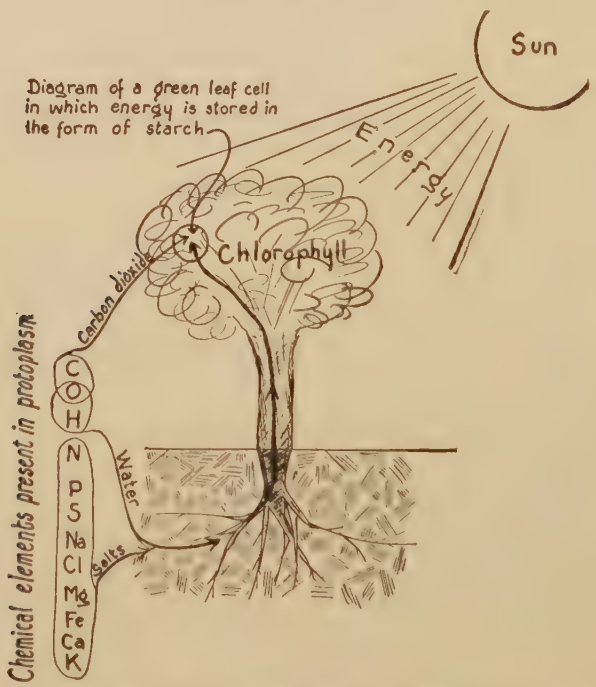


FIG. 485.—The "Aladdin's lamp" of chlorophyll.

food of both animals and plants, are well-nigh universal in distribution in the form of carbon dioxide in the air, and of water, with various dissolved salts, in the soil (Fig. 485), while sunlight, the primal source of all energy possessed by organisms of every kind, shines alike upon plant and animal. The essential difference between plants and animals with reference to locomotion, is that green plants by the aid of *chlorophyll*, that makes them

green, are able to build up into organic foods, these inorganic compounds so universally distributed, thereby imprisoning the sun's energy. Since they can do this in a stationary position they do not need to move about for their daily bread. Most animals, on the contrary, without the Aladdin's lamp of chlorophyll, must seek their food, directly or indirectly, wherever plants have made it, or perish. Hence the necessity for animal locomotion.

2. The Evolution of Locomotor Levers

As has already been said, the evolution of locomotor devices in the animal kingdom shows that as soon as vertebrates emerged from water to land, legs became necessary to serve as supporting movable levers to propel them forward over the ground, since they could no longer swim fish-fashion by stroke of the tail.

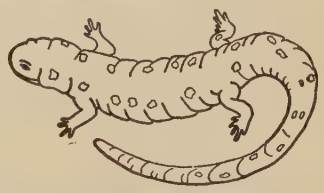


Fig. 486.—A salamander, showing weak lateral legs which push the body along without lifting it off the ground. (After Morse.)

The way in which these locomotor levers are now employed is obviously the result of an evolutionary process. It took time for the lateral legs of primitive land vertebrates to assume a vertical position and to evolve sufficient strength to raise the body off the ground. In elongated animals like salamanders and alligators, for example, there is little attempt to bear the weight of the body on the legs. Since these appendages extend somewhat laterally, like oars from a boat, they are utilized principally to push the animal along, while the weight of the body rests upon the ground (Fig. 486). After the weight-bearing function of the legs became established, Nature tried many experiments in locomotor levers, all the way from the sprawling plantigrade foot of the bear (Fig. 487), to that of the wonderfully specialized horse, which stands stilted on the tip of a single digit at the end of each leg (Fig. 488).

Fig. 487. — The plantigrade foot of a bear. (After Schmeil.)

Fig. 488. — The unguligrade foot of a horse.

Vertebrate appendages may be paired or unpaired. The latter

sort are confined to water animals and are the more primitive, taking the form of *median fins* which are either continuous, as in amphioxus and the cyclostomes, or broken up into separate dorsal, caudal, and ventral fins (Fig. 16).

3. Kinds of Appendages

In addition to median fins, fishes have two pairs of *paired fins*, namely, *pectoral* and *pelvic*, which are homologous with the locomotor appendages of land vertebrates. Since the paired fins take no part in bearing the weight of the body, they are not placed like the legs of a quadruped, but instead may appear on the sides of the body at widely varying positions in different species. The pectoral appendages tend to shift backward with the formation of the neck, while the pelvic appendages move forward. This migration from the expected position is particularly true of the pelvic fins, so that in a case as extreme as that of the cod, *Gadus*, the pelvic fins are anterior even to the pectoral fins. In other words, the "hind legs" of a codfish are in front of its "front legs" (Fig. 489).

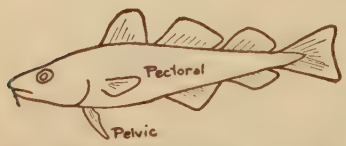


FIG. 489. — Outline of a codfish, *Gadus*, the hind legs (pelvic fins) of which are in front of the front legs (pectoral fins.)

Both the unpaired and paired fins of the fishes are used for balancing and steering rather than for locomotion.

No vertebrate has more than two sets of paired appendages and several have only one, for example, whales, sea cows, and that famous wingless New Zealand bird, *Apteryx*, while a few, notably snakes, cæcilians, and legless lizards, lack appendages of any kind.

4. Homology and Adaptation

The paired appendages of each vertebrate are built on the same plan, that is to say, are made up of the same sequence of bones which consists typically of first, a tripod of bones, known as the *girdle*, which anchors the appendage firmly to the backbone; second, a large, shaftlike bone, called the *humerus* or *femur*, according to its occurrence in the anterior or posterior pair of appendages; third, two long bones, side by side, called the *radius* and *ulna*, respectively, in the anterior appendage, and the *tibia* and *fibula* in the posterior; fourth, a complex of several small bones, making the *wrist* or *ankle;* fifth, a set of five long slender bones forming the *palm*

and *sole;* and sixth, at the tip of these long slender bones, two or three small bones placed end to end, known as the *phalanges.*

A diagrammatic representation of the sequence of bones in a vertebrate appendage, is shown in Fig. 490.

Each bone of any appendage has its counterpart not only in the appendage on the opposite side but also in the appendage in front of, or behind it, as the case may be. The similarity from side to side is spoken of as *bilateral homology* while antero-posterior correspondence of parts is called *serial homology.* Not only may homology between the bones that make up the locomotor appendages of a single individual be established *inter se,* but the leg or arm bones of one vertebrate may be homologized with those of an entirely different species of quite unlike external aspect. For example, each bone in the flipper of a whale or seal, as well as in the wing of a bat or bird, or even in the foreleg of a horse or dog, has its homolog in the human arm.

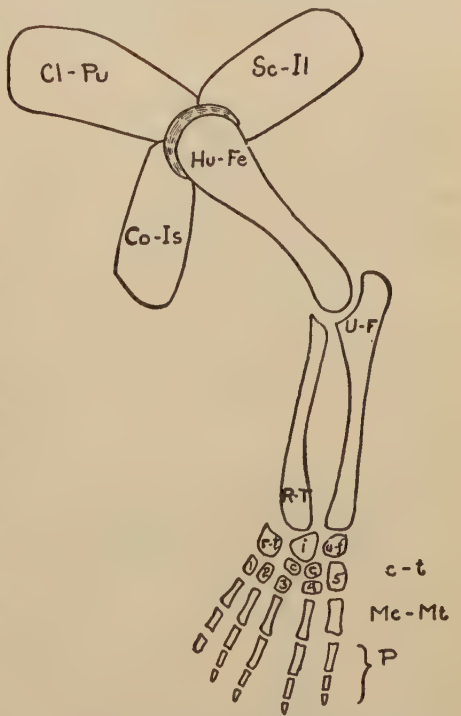


Fig. 490.—Diagram showing the homologies of vertebrate appendages. *Cl-Pu,* clavicle-pubis; *Sc-Il,* scapula-ilium; *Co-Is,* coracoid-ischium; *Hu-Fe,* humerus-femur; *U-F,* ulna-fibula; *R-T,* radius-tibia; *r-t,* radiale-tibiale; *i,* intermediale; *u-f,* ulnare-fibulare; *c-c,* centrale; *1–5, c-t,* carpale-tarsale; *Mc-Mt,* metacarpale-metatarsale; *P,* phalanges.

The great diversity in vertebrate appendages that are all fundamentally alike, is associated with the wide range of function which they perform, since climbing trees, burrowing in the ground, swimming in water, jumping, flying, running, standing, striking, lifting and grasping things, as well as many other kinds of activity, call for peculiar modifications of the type.

5. The Girdles in General

The *girdles*, or intermediary bones on either side between the body and the limbs, are each originally made up of three bones (Fig. 490), which meet in the form of a tripod at a common point where the free limb articulates.

In the *pectoral*, or anterior girdle there is no articular connection with the main axial skeleton. The girdle is laced to the anterior part of the thoracic basket by means of muscles and ligaments, and, while it may articulate with the sternum as in man, it never does so with the backbone. The *pelvic*, or posterior girdle, on the contrary, articulates with the backbone, frequently through the medium of the sacral "ribs" (Fig. 438). This difference in attachment gives a greater range of motion to the pectoral appendages and a firmer support to the pelvic appendages, which in most cases bear the greater part of the weight of the body.

The three girdle bones of each pectoral appendage occupy homologous positions with respect to the girdle bones of the pelvic appendages. Thus, one bone, respectively the *scapula* or the *ilium*, extends dorsally; another, the *procoracoid* or the *pubis*, antero-ventrally; and a third, the *coracoid* or the *ischium*, postero-ventrally.

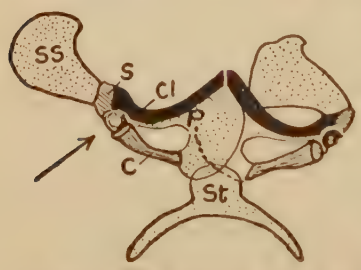


FIG. 491.—The pectoral girdle and sternum of a European toad, *Bombinator*, showing the clavicle, in black, taking the place of the procoracoid. *SS*, suprascapula; *S*, scapula; *Cl*, clavicle; *P*, procoracoid; *C*, coracoid; *St*, sternum. (The arrow points to the glenoid cavity where the arm is articulated.) (After Wiedersheim.)

The articular cup for the front leg, at the junction of the three pectoral girdle bones, is called the *glenoid cavity*, while the corresponding articular fossa on the pelvic girdle for the reception of the hind leg, by reason of its hollow shape, has been named the *acetabulum*, or "vinegar cup."

Although at first modeled in cartilage, all these girdle parts afterwards become replaced by bone. They therefore belong to the category of replacing bones, similar to those of the inner skull with the exception of certain additional investing bones in the pectoral girdle of fishes and of one investing bone, which makes up a part of the pectoral girdle of the higher vertebrates including

man. This latter bone is the *clavicle*, an antero-ventral bone without a cartilaginous ancestry, that has been substituted for the procoracoid. The fact that it is not a transformed procoracoid but instead a new bone of entirely different origin, is proved by the pectoral girdle of a European toad, *Bombinator* (Fig. 491), in which the procoracoid and clavicle are both present at the same time.

6. Comparative Anatomy of the Girdles

A. Pectoral Girdle

The pectoral girdle is somewhat more complicated than the pelvic girdle, not only because of its secondary relations with the sternum, but also since investing as well as replacing bones take part in its formation, and because it is never involved with any ventral skeletal part corresponding to the sternum.

There are no girdles either in amphioxus or cyclostomes, so the point of evolutionary departure for the pectoral girdle, as of so many other anatomical features, is found in the elasmobranch fishes, where a horse-shoe-shaped cartilage, with its points extending upwards, hooks under the "throat" just posterior to the gill arches. The pectoral fins articulate on either side of this inverted arch, about midway from the tip to the point of junction of the two sides where there are slight projections. The part above the attachment of the fin on either side (Fig. 178), is the *scapular region*, while that below, which joins the two halves of the arch ventrally, is the *coracoid region*. In skates and rays, but not in sharks, the dorsal ends of the scapular region may articulate with the most posterior branchial arch, thereby establishing an indirect connection with the axial skeleton, an unusual condition among vertebrates.

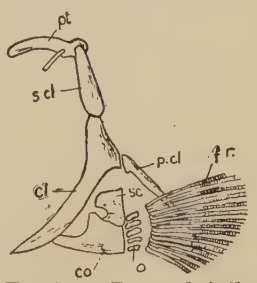


Fig. 492.—Pectoral girdle and fin of a teleost. *o*, ossicles; *co*, coracoid; *cl*, clavicle; *f.r.*, fin rays; *p.cl*, postclavicle; *pt*, posttemporal, connecting with the skull; *sc*, scapula; *s.cl*, supraclavicle. (After Folsom.)

The pectoral girdle of ganoids, dipnoans, and teleosts begins, as in elasmobranchs, with the formation of a cartilaginous arch which becomes later overlaid by investing bones. The dorsal scapular region is supplemented by a *cleithrum* or *supraclavicle*, and the ventral coracoid region by a *clavicle*. In the higher ganoids and teleosts (Fig. 492), the investing bones which pre-

dominate are described as clavicles by Bütschli and as cleithra by Gegenbaur. Whichever terminology is correct, they actually form a chain of investing bones that may connect even with the skull. In teleosts the coracoid and scapula ossify, although the investing bones on the outside make up the bulk of the girdle.

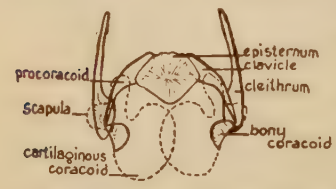


Fig. 493.—Ventral view of the shoulder girdle of an extinct stegocephalian, *Belosaurus*. The probable arrangement of the missing cartilaginous parts is indicated by the dotted outline. (After Credner.)

The fossil Stegocephali have only the bony parts of the pectoral girdles left to tell the tale, but these include coracoids, a pair of clavicles and either cleithra or supraclavicles (Fig. 493).

In urodeles the two halves of the girdles develop separately as cartilaginous plates, with a dorsal extension, the *scapula*, and two ventral processes, the *procoracoid* being anterior in position, and the *coracoid*, posterior. At the junction of these three regions on either side the anterior appendage articulates in a hollow, the *glenoid cavity*, instead of on a prominence, as in the elasmobranchs. The two halves of the girdle remain unfused throughout life, although they meet ventrally and the coracoids overlap. Later the scapular region ossifies near the glenoid cavity to form the bony scapula, leaving an unossified part of the cartilage which is termed the *suprascapula* (Fig. 494).

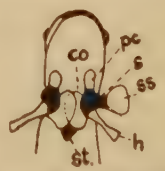


Fig. 494.—Diagram of the shoulder girdle of a urodele. *co*, coracoid; *h*, humerus; *pc*, procoracoid; *s*, scapula; *ss*, suprascapula; *st*, archisternum. (After Wiedersheim.)

Among Anura the median margins of the coracoid and procoracoid cartilages coalesce on each side into an *epicoracoid cartilage* (Fig. 444). In toads the epicoracoids overlap, or slip past each other, after the manner of coracoids in urodeles, but in frogs they abut upon each other or fuse into a common *epicoracoidal plate*. The procoracoid becomes overlaid by an investing bone, the *clavicle*, which eventually takes its place. Both the coracoid and the scapula ossify, and even the suprascapula in part, so that there finally results the following paired bones in the pectoral girdle of the frog, namely, clavicles, coracoids, scapulas, and suprascapulas, together with the epicoracoidal plate, of

which only the clavicles are investing in character. The ventromedial ends of the clavicles and coracoids are joined by the cartilaginous epicoracoidal plate, and this also fuses with the sternal elements to form a continuous ventral archisternal skeletal structure.

In general the pectoral girdle of reptiles is more bony than that of amphibians. The procoracoid remains only in turtles, its place being definitely assumed by the investing clavicle, while in chameleons and crocodiles the clavicle, although appearing in the embryo, does not develop. In intimate relation with the pectoral girdle in both crocodiles and lizards, there is present a T-shaped episternum, and the coracoid of the latter is frequently fenestrated, that is, broken up into parts that suggest, but are not homologous with separate procoracoid and coracoid elements (Fig. 445).

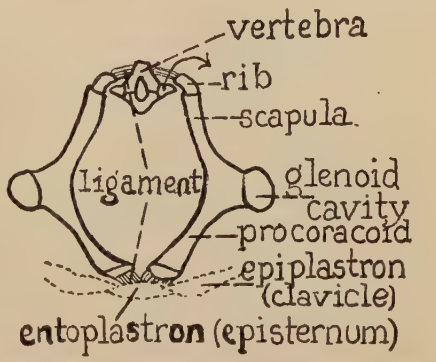


Fig. 495.—Pectoral girdle of *Chelone*, one day old. The ribs later extend in the direction of the arrows, and the girdle comes to lie *inside* them instead of outside, as in most vertebrates. (Modified from W. K. Parker.)

The pectoral girdle of turtles is peculiar. The whole structure, as well as the pelvic girdle, is *inside the ribs* which form the shell, an arrangement not attained by any other vertebrate. In the embryo the girdles are still outside (Fig. 495), but as the first and last costal plates spread to form the shell, they sink in and are covered over by the expanding ribs. There is no investing clavicle in the turtle's pectoral girdle, and the three ossified replacing bones, procoracoid, coracoid, and scapula, all pillar-like in form, come together like tripods for the support of the anterior legs.

In snakes the absence of girdles of any kind, and of appendages is correlated with the extreme lengthening of the body, and in legless lizards as well as cæcilians, with the burrowing habit, rather than with a manifestation of primitive conditions, as in amphioxus and cyclostomes.

The pectoral girdle of birds, which is completely ossified, mi-

grates farther backward from the head region than in any other kind of vertebrates. The scapula becomes reduced to a narrow swordlike bone that lies close to the ribs along the dorsal aspect of the thoracic basket; the coracoid is enlarged into a stout, beamlike bone that braces against the upper edge of the sternum; while the clavicles join with the interclavicular element, the *furcula*, into a "wishbone" that also anchors in most cases onto the sternum, thus making a firm skeletal foundation for the wings. The *glenoid cavity*, or the point on either side where the wings are mechanically attached to the whole apparatus, is partly on the scapula, and partly on the coracoid, thus insuring adequate articulation (Fig. 496). Ratitates, or running birds, show adaptive differences, as compared with carinates, or flying birds, for both coracoid and scapula are reduced and anchylosed together, and the abbreviated clavicles do not meet in a furcula. In *Pachyornis*, an extinct "moa," the shoulder girdle is entirely absent, and in the living wingless *Apteryx*, extremely rudimentary.

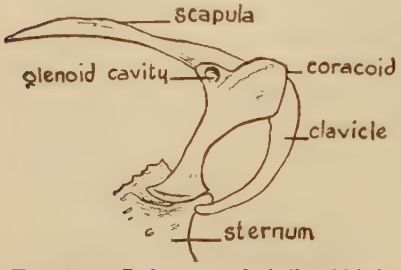


Fig. 496.—Left pectoral girdle of bird.

There are two types of pectoral girdles in mammals, as found in monotremes and higher mammals. Monotremes retain the coracoids, and have a lizardlike investing episternum intimately connected with the pectoral girdle, while the scapula also is quite unmammalian in appearance (Fig. 449). In other mammals the coracoid is wanting, except in the form of a *coracoid process*, which may remain for some time as a separate skeletal element before its final fusion with the scapula. The scapulas become the sole bearers of the anterior appendages and are broadened usually into thin triangular bones, each characterized by a keel-like ridge, the *spina scapulæ*, for the attachment of muscles (Fig. 497). The spina scapulæ has no cartilaginous antecedent and may possibly be homologized with the investing cleithra of

Fig. 497.—The left shoulder blade, as seen from behind. *A*, acromion; *C*, coracoid process; *Sp*, spina; *Sc*, scapula. (Drawn by W. Pickles.)

fishes. In mammals, such as bats and primates in which there is great freedom of movement in the anterior appendages, the clavicles are strong and well developed, connecting the scapula with the sternum. In mammals like ungulates, sirenians, and cetaceans, they are weak or absent, and in cats, merely degenerate, splintlike, floating bones, unattached at either end, so that the scapulas may be seen slipping up and down past each other under the loose skin as the animal walks.

B. Pelvic Girdle

The pelvic girdle has nothing corresponding to the thoracic basket with which to become involved and, as has been stated, is solely replacing in character. Like its pectoral homolog it consists typically of three paired parts, a dorsal element, the *ilium*, and two ventral ones, of which the *pubis* is anterior, and the *ischium* posterior, forming tripods on either side for the articulation of the hind legs (Fig. 490). This typical relation is not attained at once in the vertebrate series, and when established undergoes some striking modifications.

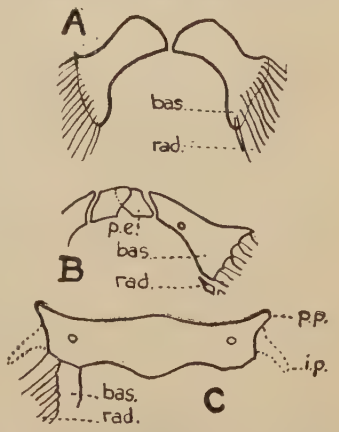


Fig. 498.—Evolution of the pelvic girdle in fishes. *A*, a fossil elasmobranch, *Pleurocanthus; B*, a ganoid, *Scaphirhynchus; C*, a modern elasmobranch. *bas.*, basalia; *i.p.*, iliac process; *pp*, pubic process; *p.e.*, pelvic elements; *rad.*, radialia. (After Wiedersheim.)

The pelvic girdle in fishes, when present, is very simple, serving merely as a support for the pelvic fins without making connection with the axial skeleton. In elasmobranchs and cartilaginous ganoids it is a flat ventral bar of cartilage (Fig. 498, C), the origin of which is suggested by *Pleurocanthus*, a fossil elasmobranch (Fig. 498, A), as well as by certain teleost fishes, in which two enlarged basal elements of the pelvic fins approach each other on the ventral side of the body, although not uniting. The cartilaginous ganoid, *Scaphirhynchus*, (Fig. 498, B), perhaps represents the connecting link between this primitive condition and the cartilaginous pelvic bar of elasmobranchs, for here the two basal elements unite, each contributing a half

to a small intermediate element. In the Holocephali these two parts do not fuse but are connected by a ligament, and each bears a dorsally directed projection, the *iliac process*.

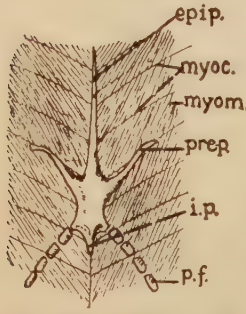


FIG. 499.—Ventral view of the pelvic girdle of *Protopterus*. *epip.*, epipubic process; *i.p.*, ischiatic process; *myoc.*, myocommata of connective tissue; *myom.*, muscular myomeres; *prep.*, prepubic process; *p.f.*, pelvic fin. (After Wiedersheim.)

The Dipnoi, as represented by *Protopterus* (Fig. 499), have a median cartilaginous plate of bilateral origin serving as a pelvic girdle, with six processes extending from it. This plate, as also the cartilaginous bar of elasmobranchs, may be called the *ischiopubic plate*. The prolonged anterior process, which lies along the midventral *linea alba*, is the *epipubic process*, and the posterior extension at its opposite end, the *hypoischiatic process*. Of the two paired sets of processes the more anterior, lying between the lateral muscles of the body wall, are the *prepubic processes*, while the more posterior short projections, to which the pelvic fins are attached, are the *iliac processes*.

Urodeles possess a cartilaginous ischiopubic plate similar to that of the Dipnoi, with an improvement in the form of *ischium bones*, which replace the cartilage in the pos-

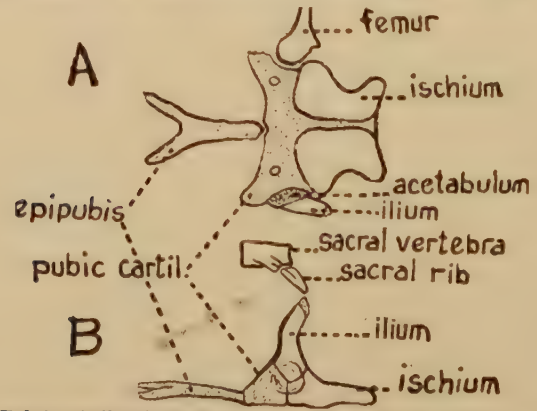


FIG. 500.—Pelvic girdle of a salamander, showing sacral rib. *A*, ventral; *B*, lateral. (The cartilage is dotted.) (After Wiedersheim.)

terior region, while the iliac processes, now become *iliac bones*, except in *Proteus* and *Amphiuma*, reach the second sacral vertebra,

joining it by means of two small intermediary parts, the *sacral ribs* (Fig. 500). In place of the prepubic process of the Dipnoi, but not homologous with it, there appears in all lung-breathing urodeles, an independent Y-shaped cartilage, the *ypsiloid cartilage*, that connects secondarily with the pelvic girdle and has to do with the function of breathing. There is also a perforation, the *obturator foramen*, on either side of the anterior, or pubic, part of the ischiopubic plate.

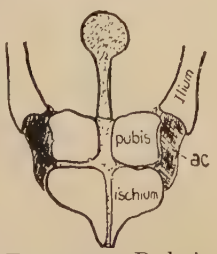


FIG. 501. — Pelvic girdle of South American toad, *Dactylethra*. *ac.*, acetabulum. (After Wiedersheim.)

In Anura there is considerable modification of the pelvic girdle due to hopping and jumping methods of locomotion. The South American toad, *Dactylethra* (Fig. 501), shows a generalized pelvic girdle with the three pairs of contributing bones all typically ossified from the cartilaginous plate, as well as the ypsiloid cartilage, which in this case is not forked in shape. In the frog, *Rana*, the three pairs of bones form a Y-shaped structure that connects the jumping legs with the single sacral vertebra. The legs are articulated on either side of a round disc, which is made up of components from all three pelvic bones so concentrated that the obturator foramina are obliterated. From this disc spring a pair of swordlike processes, the *ilia*, that reach the vertebral column, which teeters up and down between their tips, absorbing in part the shocks that would otherwise reach the brain when the jumping frog lands (Fig. 502).

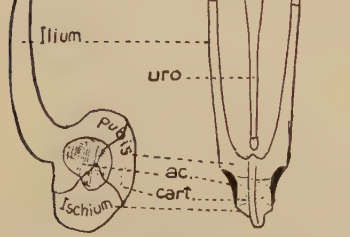


FIG. 502.—Pelvic girdle of frog, *Rana*. *A*, right lateral half; *B*, dorsal view with posterior part of vertebral column. *ac.*, acetabulum; *cart.*, cartilaginous part of pubis; *sac. v.*, sacral vertebra; *uro*, urostyle, or last vertebra. (After Wiedersheim.)

In the reptiles less cartilage remains unossified and all of the pelvic bones are distinct. There is a symphysis, or union, of both pubic and ischiac bones, along the mid line in lizards and turtles, whereas in crocodiles only the ischiac symphysis occurs, the pubic bones remaining wide open. The large space between the pubis and the ischium on either side is termed the *ischiopubic foramen*. There is an obturator

foramen in *Sphenodon* (Fig. 503), and the lizards, but in turtles and crocodiles it combines with the ischiopubic foramen into a common opening separated from its mate on either side by a median ligament. The articular cup, or *acetabulum*, formed at the junction of the three pelvic bones for the articulation of the hind leg, is perforated in crocodiles, birds, and monotremes. Small epipubic and hypo-ischiatic elements, which are absent in crocodiles, retain their identity in lizards and turtles. The ilium in crocodiles tends to widen, fore and aft, so as to enclose a larger number of vertebræ, a tendency which becomes excessive in birds.

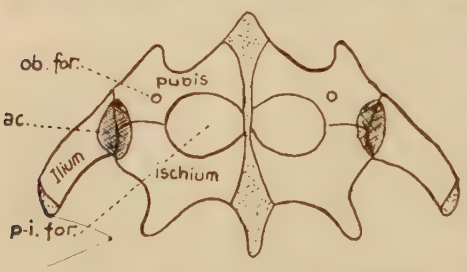


Fig. 503.—Ventral view of pelvic girdle of *Sphenodon*. *ac.*, acetabulum; *ob. for.*, obturator foramen; *p-i. for.*, pubo-ischiac foramen. (After Wiedersheim.)

The separate bones of a bird's pelvic girdle (Fig. 504), become not only fused with each other, but also through the ilium, with a comparatively large number of sacral vertebræ, thus furnishing support for the weight of the body upon the hind legs. The acetabulum, as in crocodiles, is perforated.

Fig. 504.—Pelvic girdle of a hen. (After Leche.)

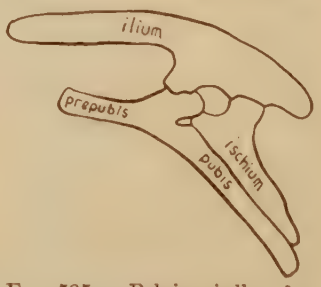


Fig. 505.—Pelvic girdle of a dinosaur, *Stegosaurus*. (After Marsh.)

The dinosaurs among the reptiles prophesied the modifications which characterize the pelvic girdle of birds. For instance, the girdle of the fossil reptile *Stegosaurus* (Fig. 505), shows a spreading fanshaped ilium, a long ischium extending posteriorly without a symphysis, and a pubis that runs parallel to it, instead of meeting anteriorly and ventrally in a symphysis. The place of the pubis is partly assumed by a prepubic process. Modern birds exemplify

all of these features, with the ilium enormously expanded and the prepubic process reduced or absent. In the embryo of the bird the bones extend transversely, approaching each other as if a symphysis or junction was to follow (Fig. 506), but by the time the adult condition is reached, they have spread apart and come to project backward, as in *Stegosaurus*, thus allowing for an unhindered passage of large eggs with breakable calcareous shells. Long before the American Museum expeditions to Mongolia unearthed the famous dinosaur eggs that now repose in the American Museum of Natural History in New York City, the spreading pubic bones of these fossil animals made it possible to guess that they laid calcareous eggs.

FIG. 506.—Pelvic girdle of an embryo bird, showing the natural position of the pubis before its backward migration. (After Mehnert.)

The primitive character of *Archæopteryx*, is clearly shown in the pelvic region, as the girdle bones are small, the sutures between them remaining open, and the ischia do not extend backward in the pronounced way of modern birds, but meet in a symphysis, while the ilium connects with only six sacral vertebræ.

In mammals the three embryonic bones on either side of the pelvic girdle fuse together to form the *innominate bones*, which meet ventrally at the *symphysis pubis* (Fig. 507). In monotremes, marsupials, many rodents and insectivores, ungulates, and carnivores, there is a *symphysis ischiaticum* as well as a symphysis

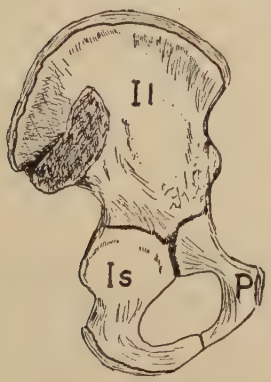


FIG. 507.—Inner surface of the innominate bone of a child of eight years, showing the component parts. *Il*, ilium; *Is*, ischium; *P*, pubis. (After Morris.)

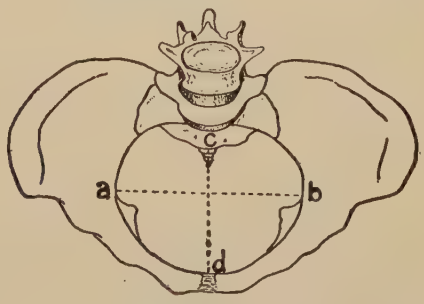


FIG. 508.—Outline of the female pelvis. *a-b* and *c-d*, two diameters of the pelvic opening. (After Cunningham.)

pubis, but in primates the ischia separate, giving two skeletal points of support to the sitting animal. It would be extremely awkward for a cow, even were she so minded, to "sit down" upon the single edge formed by the fusion of the two ischia.

The large common opening formed by the two innominate bones, is both the ischiopubic and obturator foramina in one (Fig. 508). Through this bony halo must pass every mammal that is normally born into the world. There are some distinguishable differences in this opening in the two sexes, the average comparative dimensions in man, according to Rauber, being as follows:

	a to b	c to d
♂	12.7 cm.	11.2 cm.
♀	14.5 cm.	12.7 cm.

Monotremes and marsupials have a pair of additional pelvic bones, the *marsupial bones*, projecting forward from the pubis. Although perhaps useful in supporting the marsupial pouch of the female, they are not primarily for that purpose, since they are equally well developed in both sexes. They are probably homologous with the epipubic bones of lower vertebrates, for no trace of them occurs in placental mammals.

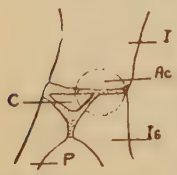


Fig. 509.—Pelvic girdle of a civet cat, *Viverra*, showing the cotyloid bone. *Ac*, acetabulum, in dotted outline; *C*, cotyloid bone; *I*, ilium; *Is*, ischium; *P*, pubis. (After Wiedersheim.)

The *cotyloid bone*, a fourth small bony element which enters into the formation of the acetabulum in mammals (Fig. 509), ossifies later than the other components.

7. The Free Appendages

Homologies between the girdles and the free appendages attached to them are indicated in the table on page 557, in which the synonyms of the names employed for the various parts are included.

A. Unpaired Fins

The locomotor appendages of vertebrates may be grouped into *single* and *paired lateral* appendages. The former type reaches its highest manifestation in the unpaired fins of fishes.

THE HOMOLOGIES OF THE GIRDLES AND OF THE FREE APPENDAGES

	Pectoral			*Pelvic*	
COMMON NAME	TERMS USED IN HUMAN ANATOMY	TERMS USED IN COMPARATIVE ANATOMY		TERMS USED IN HUMAN ANATOMY	COMMON NAME
	Scapula	Scapula	Ilium		
Shoulder		Procoracoid	Pubis	Innominate Bone	Hip
	Clavicle	Clavicle			
	Coracoid Process	Coracoid	Ischium		
Upper Arm	Humerus	Humerus	Femur	Femur	Thigh
Fore Arm	Ulna Radius	Ulna Radius	Fibula Tibia	Fibula Tibia	Shank
	Naviculare (Scaphoid)	Radiale	Tibiale	Talus (Astragulus)	
	Lunatum (Semilunar)	Intermediale	Intermediale		
	Triquetrum (Cuneiform)	Ulnare	Fibulare	Calcaneus (Calcis)	
		Centrale I Centrale II	Centrale I Centrale II	Naviculare	
Wrist	Multiangular majus (Trapezium)	Carpale I	Tarsale I	Cuneiform I (Ento-cuneiform)	Ankle
	Multiangular minus (Trapezoid)	Carpale II	Tarsale II	Cuneiform II (Meso-cuneiform)	
	Capitatum (Magnum)	Carpale III	Tarsale III	Cuneiform III (Ecto-cuneiform)	
	Hamatum (Unciform)	Carpale IV Carpale V	Tarsale IV Tarsale V	Cuboid	
	Metacarpale I	Metacarpale I	Metatarsale I	Metatarsale I	
	" II	" II	" II	" II	
Palm	" III	" III	" III	" III	Instep (Sole)
	" IV	" IV	" IV	" IV	
	" V	" V	" V	" V	
	Phalanges (5)	1st row	Phalanges (5)	1st row	
Fingers	" (5)	2nd "	" (5)	2nd "	Toes
	" (4)	3rd "	" (4)	3rd "	

The forerunner of the median appendages is seen in amphioxus, where a continuous fin, or integumental fold, supported by connective tissue (Fig. 16), extends from the anterodorsal region around the end of the tail, and ventrally to the left of the anus as far forward as the atrial pore (Fig. 15). A similar continuous median fin is characteristic of most fishes in early embryonic stages. As development proceeds, portions of this continuous fin are absorbed, leaving parts which form the various *dorsal*, *caudal*, *anal*, and *ventral* fins. In general these median fins serve, like the centerboard of a catboat, to maintain an even keel in water. The caudal fin also increases the effectiveness of the lateral stroke of the tail in locomotion.

The most primitive type of a tail in fishes is *diphycercal* (Fig. 510, A), in which the vertebral column remains unbent, and the

inconspicuous flanges of the caudal fin are practically equal, ventrally and dorsally. In elasmobranchs and some ganoids the end of the skeletal axis curves upward (Fig. 510, B), and the ventral flange of the caudal fin becomes considerably larger than the dorsal portion. This condition is termed *heterocercal*. The great majority of fishes, however, have a *homocercal* arrangement, in which the upturned end of the skeletal axis becomes reduced or obliterated, and the dorsal flange of the caudal fin comes secondarily to equal the ventral part. Frequently the caudal fin is deeply incised, as in the mackerel, *Scomber* (Fig. 510, D), or more or less rounded, as in the "mummichug," *Fundulus* (Fig. 510, C).

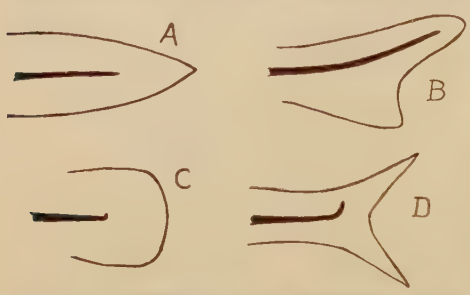


FIG. 510. — Different types of tails in fishes. *A*, diphycercal; *B*, heterocercal; *C*, *D*, homocercal.

The fins of fishes are braced in position by skeletal elements which lie between the two walls of the fin fold. The innermost of these supporting elements (*basalia*) connect with the neural spines of the underlying vertebræ, while the outermost ones (*radialia*) splice onto the basalia. In addition in many fishes there is a third kind of skeletal fin rays overlapping the radialia (*actinotrichia*) which are horny in texture, epidermal in origin, and double in structure (Fig. 178), one half being derived from either side of the fold of skin constituting the fin. The actinotrichia may entirely replace the radialia, while both radialia and basalia, whether cartilaginous or bony, may appear in the same species of fishes. Frequently isolated basalia, usually situated directly in front of the fin proper, develop into spines that become organs of defense.

Amphibian larvæ, as well as adult perennibranchs, have a caudal fin that may extend some distance anteriorly, but differs from the corresponding caudal fin of fishes in being without skeletal support.

Sirenians and cetaceans also develop caudal fins, which, like those of amphibians, are without internal skeletal support, and not homologous with those of fishes, being horizontal rather than vertical in arrangement.

B. Lateral Appendages in General

Typically there are two pairs of lateral appendages in vertebrates which, although not strictly metameric in origin as are the paired appendages of invertebrates, like them serve a great variety of uses aside from the primary function of locomotion.

Of vertebrates without paired appendages, amphioxus and the cyclostomes represent a primitive condition. Other legless vertebrates, such as the apodans, snakes, and certain lizards, when adult, are reduced secondarily to this state, for some at least have appendages in their early stages. P. and F. Sarasin, for example, have found legs in the embryo of the apodous amphibian, *Gymnophiona*.

A few vertebrates have only anterior appendages. The list includes the ganoid, *Calamoichthys;* representatives of the teleost order of Apodes; the urodele, *Siren;* the lizard, *Chirotes;* the Sirenia; the Cetacea, although Kükenthal found hind legs in the embryo of one species of whale; and some other forms.

A smaller list of vertebrates, with posterior appendages only, includes pythons and boa-constrictors with rudimentary hind legs embedded in the skin; the lizards, *Pygopus* and *Pseudopus*, and possibly some other forms. The Australian burrowing "kiwi," *Apteryx*, although regarded as wingless, shows vestigial anterior appendages.

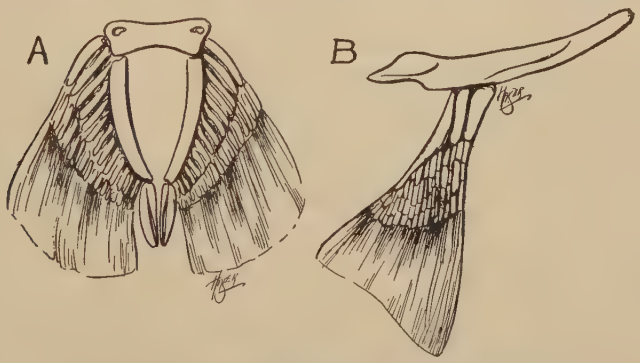


Fig. 511.—Girdles and paired appendages in an elasmobranch. *A*, pelvic; *B*, pectoral.

C. Different Pectoral Appendages

The pectoral appendages of fishes are of two general types, represented by the elasmobranchs and the dipnoi. In the former a chain of enlarged cartilages, the *pros-*, *mes-*, and *metapterygia*, articulate the fin with the girdle (Figs. 178 and 511), and bear whatever

fin rays, basalia, radialia, or actinotrichia, may complete its skeletal foundation. In the latter type, there is a certain chain of skeletal elements, with fin rays equally displayed on either side (Fig. 512). In fins of either type, joints between the parts are reduced to a minimum, since rigidity of the flat fin, moving as a unit, is the desideratum in a water medium.

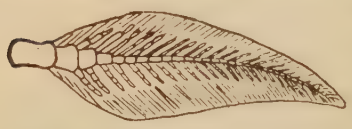


FIG. 512.—Diagram of the anterior fin, archipterygium, of *Neoceratodus*. (After Galloway.)

Beginning with the urodeles, all higher vertebrates have a typical pair of lateral anterior appendages (see Table on page 557), each consisting of a single long bone, the *humerus*, articulating with the girdle; a pair of long bones, the *radius* and *ulna;* at least two rows of wrist bones, *carpalia;* five palm bones, *metacarpalia;* and finally, digit bones, or *phalanges*. These bones are all joined together as a system of levers which, with their accompanying muscles, become effective means of locomotion.

FIG. 513. — Tarsus of a salamander, *Cryptobranchus*. *f*, fibulare; *i*, intermediale; *t*, tibiale; c^1c^2, centralia; *1–6*, distal row of tarsals; *I–V*, metatarsals. (After Wiedersheim.)

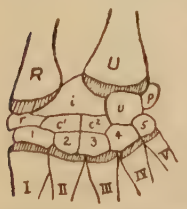


FIG. 514.—Carpals of *Sphenodon*, showing two *centrale* bones. *R*, radius; *U*, ulna; *r*, radiale; *i*, intermediale; *u*, ulnare; c^1 and c^2, centralia; *1–5*, carpale bones; *I–V*, metacarpalia; *P*, pisiforme, a sesamoid bone. (From Wiedersheim, after Baur.)

In urodeles there are present four fingers instead of five, with an extra bone, the *centrale*, inserted between the two rows of carpals in the wrist (Fig. 513).

The Anura show a fusion of the radius and ulna into a single bone, the *radio-ulnar*, while the middle one of the proximal row of carpal bones, the *intermediale*, is absent.

In reptiles there is an intratarsal joint between the two rows of tarsals. *Sphenodon* has two *centrale* bones in the wrist (Fig. 514), but only one is common in other reptiles except the crocodiles, which have none. The fossil pterodactyls had an enormously elongated little finger, to which the stretched sail-like skin, serving as an organ of flight, was attached. The extinct dinosaurs and plesiosaurs had a great multiplication of phalanges to sustain their flipper-like appendages.

In birds the anterior appendages, emancipated from terrestrial locomotion, have become extremely modified into wings. The original quadrupedal character of birds is seen, however, in nestlings, which scramble about in the nest using their undeveloped wings as legs. The long bones of the bird's wing are still further lengthened, the carpals are compacted together, and the fingers are reduced in number normally to one (Fig. 416), which furnishes a rigid support for the quill feathers of flight. *Archæopteryx* points the way that this extreme evolution has taken by showing three fingers instead of one on each wing (Fig. 44). The embryonic tern, *Sterna* (Fig. 515), also shows three fingers, but most birds have become so committed to the single-fingered hand that even the tradition of a pentedactyl ancestry has been forgotten in embryonic development.

FIG. 515.—Diagram of the wing bones of an embryo tern, *Sterna*, showing traces of three fingers, in black. (After Leighton.)

The anterior appendages of mammals, which have a single basic plan, nevertheless exhibit a great variety of modifications, due to the diverse uses to which they are put. Climbing, digging, flying, striking, standing, grasping, and lifting are only a few of the many functions that make necessary structural adaptations. Even in the extremely modified flippers of the whale (Fig. 516), it is possible to homologize each of the transformed bones present with those of other mammals.

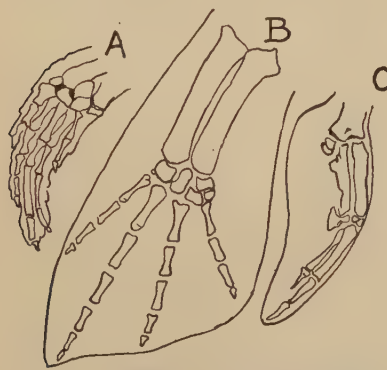


FIG. 516.—Flippers. *A*, sea turtle; *B*, whale; *C*, penguin. (After von Hanstein.)

In man the emancipated arm, freed from locomotion and support, takes on new activities. The function of the prehension of food, for instance, is no longer confined to the mouth and lips as in many animals whose arms are still legs, nor are defensive structures like horns any longer necessary, because the swinging arms take the place of such organs of defense.

D. Different Pelvic Appendages

The sequence of bones in the vertebrate pelvic appendages is homologous with that of the pectoral appendages. (See Table

Fig. 517.—Diagram of the manner in which the appendicular levers operate in a typical quadruped.

on page 557.) They are in succession, *femur; tibia* and *fibula;* two rows of *tarsals,* with *centralia* frequently inserted; *metatarsals; and phalanges.*

In general the chain of levers which these bones form, acts as a "pusher" in locomotion, while that of the anterior appendage

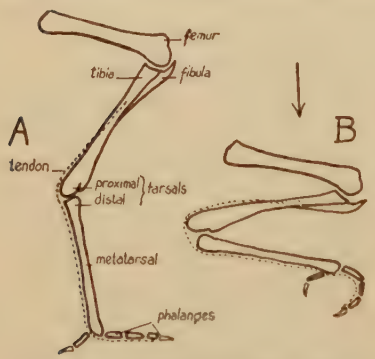


Fig. 518.—The perching mechanism of a bird. *A,* standing; *B,* perching. When a bird "squats", the leg bones jack-knife together, thus pulling the tendon of the toe taut and clinching the phalanges around the perch. To unlock the foot it is necessary for the body to be raised, thus straightening the leg and loosening the tendon. When a bird is standing up its femur is nearly horizontal and the knee joint points forward as in man during the sitting position. This makes the "take-off", or leaving the ground for flight, easier.

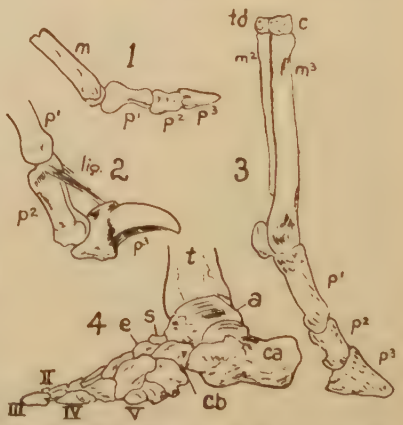


Fig. 519.—Different methods of contact with the ground. *1,* middle toe of a tapir (semi-plantigrade); *2,* dog (digitigrade); *3,* horse (unguligrade); *4, Coryphodon anax, Osborn* (plantigrade). *m,* metacarpal; *p,* phalanges; *td,* trapezoid; *c,* capitatum; *lig.* dorsal ligament; *t,* tibia; *a,* talus; *ca,* calcaneus; *s,* scaphoid; *e,* ectocuneiform; *cb,* cuboid; *II–V,* second to fifth finger. (After Weber.)

is that of a "puller" (Fig. 517). This is true both for quadrupeds on the ground and for climbers in trees.

The differentiation between the anterior and posterior appendages in birds is very great (Fig. 416). The legs assume the entire support of the body upon the ground, having become modified accordingly. The tibia and fibula fuse into a single bone with undivided responsibility, and the tarsal bones become both reduced in number and solidly joined to other skeletal parts in the interests of increased firmness and strength, the proximal row fusing with the end of the tibia, and the distal, with the metatarsals, a condition which brings the ankle joint between the two rows of tarsal bones as in many reptiles.

The arrangement of levers in the legs of a bird combines the ability to walk and run with the possibility of sudden elevation in order to "hop off" in aviation. This latter accommodation is attained through the angle that the femur normally assumes with the tibio-fibula when not in flight. It will be seen (Fig. 518), that a bird is "sitting down" while it is still standing up, since the knees are directed forward horizontally, enabling it, by straightening the legs suddenly, to rise enough at any rate to take to the air successfully.

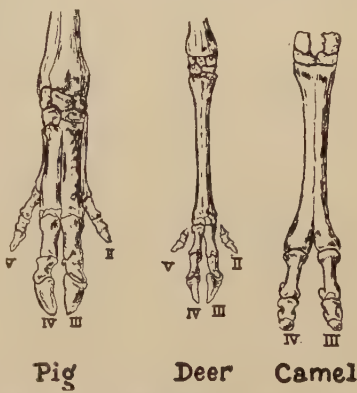


Fig. 520.—Evolution of artiodactyl foot. (After Flower.)

Among mammals the ankle joint is never between the rows of tarsal bones. The human foot, like that of the bear, is *plantigrade*, having not only phalanges and metatarsals, but even some of the tarsals in contact with the ground. Cats and dogs are *digitigrade* (Fig. 519, 2), because the ankle is lifted off the ground, while ungulates are *unguligrade*, that is, elevated on to the tips of the toes (Fig. 519, 3). The unguligrade tapir of South America rests on the ends of the four toes of each foot. The pig walks on two toes with two degenerate toes hanging on either side (Fig. 520), which may make an impression when the animal walks over soft muddy ground in which the footprints are deep impressions. Artiodactyls generally are two-toed with the other

toes in various degrees of degeneration, while perissodactyls, like the horse, are reduced to standing on the tip of a single toe on each foot. The ancestral gallery of family portraits of horses shows all intermediate degrees of evolution from the five toes of *Eohippus* to the single toe of the modern horse. Flatfooted man has a long way to go in order to reach the extreme stage of pedal evolution attained by the horse, supposing toe-dancers are prophets.

E. The Human Hand

The human hand takes part with the large brain in placing man triumphant at the head of animal creation. Without its aid the arts and sciences, which are the flower and expression of human civilization, would not have been possible.

Fig. 521. — The opposable human thumb.

The hand is first of all a grasping organ, mounted on a movable arm, that can hold a tool or grip a weapon (Fig 521). Without such artificial aids as tools and weapons, man would still be a beast, since the only devices of this kind that a beast has, like the goring horns of a bull or the chiseling teeth of a beaver, are supplied by nature as a part of the animal mechanism. Once a hand is evolved that is capable of grasping artificial aids, the invention and utilization of these devices goes forward with leaps and bounds entirely unparalled in the slow processes of the natural selection of bodily structures. As an evolutionary resource such a short cut to efficiency is an incalculable advantage to its possessor. Aside from man only the higher apes among animals make any attempt to use even so simple a tool or weapon as a stone or a stick. The idea of fashioning anything to be held in the hand for any purpose whatsoever, is entirely human.

The absolute dependence of man upon an opposable thumb and a grasping hand is the key to most of his activities. What laborer works without his hands? What artisan, even in the days of machinery, can produce anything without in some stage of the process "fingering" it? The artist who creates a painting or a statue, must hold brush or chisel, and even the prize-fighter clenches his fist, with its tightly opposable thumb, in order to earn his daily bread. The mechanical performance of all

writing and printing, with everything that this means in the communication of ideas, is primarily thumb and finger work, and the same is true of most human activites that make up what we call civilization. The common phrase, "He had a hand in it," expresses exactly and literally the part dominant man has taken in the world's affairs.

CHAPTER XVIII

PRODUCTION OF MOTION AND LOCOMOTION (MUSCLES)

I. MUSCULAR ACTIVITY

The actions of animals, which "speak louder than words," are brought about by the triple agency of nerve, skeleton, and muscle. Of this trinity of parts the muscles, or "flesh," constitute the greatest bulk, making up in man approximately half the total weight. Although the skeleton, or scaffolding, is the primary factor in determining the form of the body, the muscles that drape the skeleton are chiefly responsible for the characteristic contours which give it grace and beauty of outline.

It is essential for the surgeon to possess detailed knowledge of the separate muscles of the human body, consequently careful training in *myology*, or the science of muscles, is part of the indispensable discipline that every well-equipped medical student must undergo, but this knowledge can be attained only by careful and repeated dissections, rather than by reading descriptions of muscles in books. The general student, however, may profitably take at least a superficial comparative survey of the muscular system, which is all that will be attempted in this chapter.

Muscular activity has its morphological basis in cellular units, which, unlike inorganic substances, possess the power to increase with use. The muscle cells, although presenting nothing fundamentally new in cell structure, are specialized in the matter of *contractility* which is one of the universal properties of protoplasm.

Elastic *myofibrils*, which shorten in only one direction, appear within the muscle cell, and these are capable of causing movement not only within the cytoplasm of the muscle cell itself, but also outside of it, thus effecting both motion and locomotion.

Muscular movement is always the result of *muscular contraction*. When, for example, a leg is bent by the shortening of one

set of muscles, it is restored to its original position not by the relaxation of these muscles but by the contraction of an antagonistic set on the other side of the leg (Fig. 522).

Muscular activity, aside from effecting countless necessary movements of different parts of the body, and serving as the engine of propulsion for the animal machine, contributes in a variety of ways to the welfare of the animal organism. The exercise of the muscles constantly changes the character of the blood and lymph, since more carbon dioxide is given off from the blood during exercise than at other times; vascular congestion is decreased by the dilation of the arteries; the ventilation of the lungs is increased; the lymph flow promoted; peristalsis is stimulated; and the heart is trained to meet emergencies.

Fig. 522.—Antagonistic muscles on the human leg. (After Mollier.)

The muscles of the living body are never entirely relaxed, but maintain a condition of balanced tension, or *tonus*. For example, when the body wall is pierced by a bullet, the resulting hole is more slitlike than round, showing that the muscles are always somewhat taut.

Fatigue in muscle activity is referable to the nerve supply rather than to the muscle itself, for when a muscle becomes too fatigued to contract again, the direct application of an electric current to it will cause contraction to be resumed, which indicates that fatigue is a matter of the nervous mechanism through which the stimulus is received, rather than of the muscle itself.

II. MUSCLES AS TISSUES

Muscles may be considered either from the point of view of tissues, or of organs. There are three sorts of muscle tissues, already briefly described in Chapter VII, as smooth, striated, and cardiac, which differ from each other in origin, histological appearance, physiological action, and distribution. Each muscle cell connects with a nerve ending that controls its behavior.

Smooth muscle cells are derived from mesenchyme, and are comparatively short with a single nucleus (Fig. 89, A), being frequently isolated or combined in thin sheets. They are involuntary, slow in action, and are supplied from the sympathetic nervous system, while they occur in the skin, the wall of the digestive tract, blood vessels, urogenital passages, and ducts of various kinds. In blood vessels they are arranged mainly in circular fashion, thus decreasing the bore of the tube upon contraction, while enlargement of the lumen is effected by blood pressure. They are not supplemented by tendons, and they form parts of other organs rather than organs in themselves.

Striated muscle fibers are mesodermal in origin. They form elongated structures with many nuclei; are rapid in contraction, being under the voluntary control of the central nervous system; and constitute most of the musculature of the body, particularly the muscles with skeletal attachment.

Cardiac muscle fibers, which are intermediate between smooth muscle cells and striated muscle fibers, are of mesenchymal origin, being modified from the tunica media of an embryonic blood vessel. They are short, syncytial structures, uninucleate, and usually branched or anastomosing together, showing weak striations (Fig. 104). Unlike true striated muscle cells, they are involuntary in action. They occur in the walls of the heart, and of the pulmonary arteries and veins, and also in the roots of the aorta.

FIG. 523.—The biceps muscle, showing origin and insertion. (After Mollier.)

III. MUSCLES AS ORGANS

Striated muscle cells combine to form organs with more or less morphological and physiological unity. There is great variability in separate muscles, however, even in homologous muscles on the two sides of the same individual, as muscles are by no means such conservative structures as bones, teeth, or nerves. Testut[1] has written an impressive tome of some 900 pages, which deals mostly with anomalies found solely in the muscles of the human body.

[1] *Les anomalies musculaires chez l'homme expliquées par l'anatomie comparée leur importance en Anthropologie.* Paris, 1884.

The muscles of the limbs are often fusiform, since this type is less bulky for the amount of muscular tissue involved than some other shapes. Triangular muscles appear where there are narrow origins and broad insertions, such as is found in the *pectoralis* group. Sheet muscles occur in such situations as the diaphragm where the work to be performed is best served by this morphological form.

The *biceps muscle* may be taken as typical (Fig. 523). It consists of an enlarged middle portion, the *belly*, with tapering ends, and is surrounded by a connective tissue sheath which at the ends becomes continuous with *tendons*, that in turn merge into the *periosteum* ensheathing the bones, thus securing anchorage for the muscle. One end of the muscle, the *punctum fixum*, where it is attached to the most stationary part of the skeleton, is the *origin*. The other end, the *punctum mobile*, where it connects with the more movable part of the skeleton, is the *insertion*. Upon the contraction of any muscle the insertion is always pulled towards the origin. There may be several insertions, as in the *serratus muscles* along the back, or there may be more than a single origin; for example, two are present in the biceps, giving it the name of "biceps."

FIG. 524.—Superficial muscles of the back. (After Morris.)

Sometimes, as in the *trapezius muscle*, which moves head and shoulder, the punctum fixum may become the punctum mobile, according to the movement to be effected.

Muscles in general show a wide range of variation in form (Fig. 524), a necessary adaptation to accomplish different move-

ments. The original type of embryonic muscles shows sheets of fibers, or *myotomes*, extending between partitions of connective tissue, similar to the muscles on the sides of the body of a fish. Out of this primitive arrangement modifications are obtained (1) by delamination, or splitting flatwise; (2) by splitting lengthwise; (3) by proximo-distal division; and (4) by various degrees of fusion.

It is not always easy to identify and delimit a muscle, because of the changes brought about through functional necessity. The best criterion, however, for homologizing a muscle, is its nerve supply. A nerve once assigned to do duty with a muscle follows it through all its vicissitudes, just as a faithful dog, trotting behind its master, always serves to identify him, regardless of the different costumes or disguises which the master assumes.

FIG. 525.—The *tendon of Achilles*, in black, showing how the work which muscles do may be applied at a point some distance from the muscle itself. (Drawn by W. Pickles.)

An illustration of the constancy of the nerves is furnished by the *phrenic nerve* that supplies the diaphragm, which is a migratory muscle laid down originally far anterior in the neck region. With the backward shifting of the heart, the diaphragm comes to assume an abdominal position remote from the neck, yet the phrenic nerve, although made up from the third, fourth, and fifth cervical nerves, goes out of its way to retain connection with it and to proclaim its origin.

As already indicated, *tendons*, or sinews, are the means by which muscles are attached to bones, and in this capacity they serve a double purpose. In the first place they enable soft, delicate, contractile muscles to gain a firm, tenacious grip upon solid skeletal parts, whereby motion may be effected, while in the second place they render it possible for large muscles that make up the bulky part of the body to be packed in out-of-the-way situations, sometimes at considerable distances from the

work to be performed, where they will not interfere by their bulk with the free movement of the joints. The "tendon of Achilles" (Fig. 525), like the electric cable that transmits power generated at Niagara Falls to industries in the city of Buffalo, is a more efficient arrangement for the ankle to have, because the muscles are largely concentrated out of the way on the "calf of the leg," rather than around the ankle itself, where they would interfere with freedom of movement.

Sometimes ossifications occur within tendons at points of friction. These are called *sesamoid bones*, the most conspicuous example being the knee cap, or *patella* (Fig. 525). Rarely the entire tendon ossifies, as on the sides of a "drumstick" of a turkey.

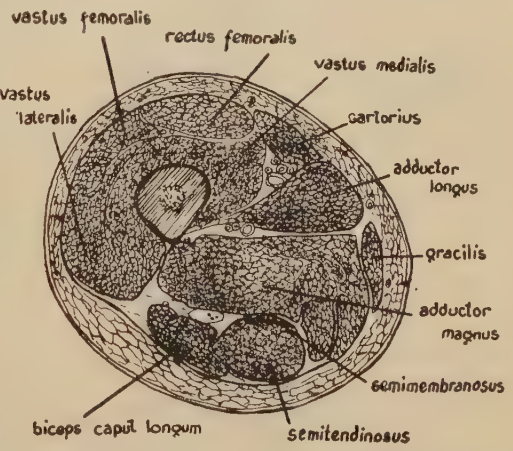


FIG. 526.—Cross section through the leg, showing the arrangement of muscles. Bone shown by parallel lines; lighter spaces between muscles are connective tissue. (After von Bardeleben.)

Muscles generally are encased in connective tissue sheaths, or *fascia*, which are more or less continuous by means of connecting tendons with similar periosteal sheaths surrounding the skeletal parts. Connective tissue elements also extend even between groups of muscle fibers themselves, separating them into irregular bundles, or *fasciculi*.

The topographical relation of neighboring muscles to each other and to the bone foundation which they surround, is typically indicated by Fig. 526, in which is represented a diagrammatic cross section of the human leg above the knee. Blood vessels and nerves are shown between the muscles.

A microscopic examination of a single muscle shows that it is made up largely of *elastic fibers* running lengthwise, which in turn are clustered together into groups or bundles that are evident in cross section and to which the name *Cohnheim areas* has been applied.

IV. EMBRYOLOGY OF MUSCLES

When the mesoderm forms in a vertebrate, there is much more of it along the dorsal side of the embryo, *epiaxially*, than on the ventral side, *hypoaxially* (Fig. 111). This is not true of invertebrates such as annelid worms, in which the mesoderm is about equal all around the body (Fig. 206). The reason for the epiaxial excess of mesoderm in vertebrates is that along either side of the notochordal region there is early formed a row of metameric sacs, or *myotomes*, which have thick inner, or splanchnic walls, from which the muscles are destined to arise, the outer, or somatic walls being set aside to form the corium of the skin (Fig. 110, D). For a time the cavity of the myotomes, which separates the splanchnic from the somatic mesoderm, is continuous with the body cavity, but later becomes separated from it and eventually is entirely obliterated (Fig. 112).

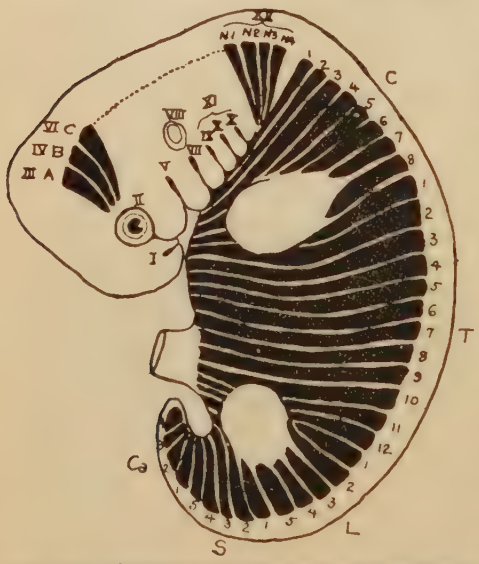


FIG. 527.—Scheme to illustrate the disposition of the myotomes in the human embryo. *A*,*B*,*C*, the first three cephalic myotomes; *N*, *1*,*2*,*3*,*4*, last persisting cephalic myotomes; *C*,*T*,*L*,*S*,*Ca*, the myotomes of cervical, thoracic, lumbar, sacral, and caudal regions. Roman numerals refer to cranial nerves. (After Cunningham.)

During these embryonic changes the muscle cells, originating in the splanchnic mesoderm of the myotome, become rearranged so that, instead of forming a cubical or columnar epithelium, their long axes come to run parallel with the long axis of the body, while between the myotomes are developed from the mesenchyme partitions of connective tissue, *myocommata*, to which the muscle cells are primarily attached. The ventral edges of the muscle plates now extend until they meet along the *linea alba*, which is a longitudinal mid ventral

line of connective tissue The end result, as shown in amphioxus (Fig. 13), is a series of zigzag muscle plates, extending along the sides of the body and separated from each other by myocommata, that are destined to form the axial muscles of the body from which the appendicular muscles secondarily bud forth as the appendages themselves push out. Even in man (Fig. 527), the embryonic arrangement of body muscles is metameric at first so that the complexities of adult musculature are derived from this primitive arrangement.

Involuntary muscles generally are mesenchymal in origin, but the muscles of the iris of the eye, as well as those associated with skin glands, are ectodermal.

V. KINDS OF VOLUNTARY MUSCLES

Wilder, who makes an excellent analysis of the comparative anatomy of the muscular system in "*The History of the Human Body*," classifies the voluntary muscles in three groups, namely, metameric, branchiomeric, and integumental.

The *metameric* group, which includes the axial and appendicular muscles, in reality takes in most of the muscles of the body. The *branchiomeric* muscles are associated with the primitive splanchnocranium and its derivatives, while the *integumental* group consists of muscles that have split off secondarily from the two preceding groups and taken up major associations with the integument rather than the skeleton.

The voluntary muscles will be briefly considered in the following order:

1. *Metameric*
   - A. Axial
     - a. Head
       1. Eyeball
       2. Hypoglossal
     - b. Trunk
       1. Ventral
       2. Dorsal
     - c. Diaphragm
   - B. Appendicular
     - a. Extrinsic
     - b. Intrinsic
2. *Branchiomeric*
   - A. Vth cranial nerve group
   - B. VIIth cranial nerve group
   - C. IXth cranial nerve group
   - D. X–XIth cranial nerve group
3. *Integumental*

1. Metameric Muscles

A. Axial Muscles

Primarily the *axial muscles*, which are the first to appear embryologically and phylogenetically, are arranged with regularity down either side of the body, fitting into each other like a nest of spoons, since they are segmental derivatives of the embryonic myotomes. There may be sixty or more pairs of these *myomeres*, as they are called, in amphioxus, varying somewhat in symmetry on both sides of the body. When their longitudinal fibers contract, they exert a pull upon the myocommata that separate them from each other, and thus upon the stiff notochord, the outer sheath of which is continuous with the myocommata.

The myomeres are all practically alike, though diminishing in size toward the end of the tail. With the advent of the head in fishes the first real modification comes, representing a fusion of an undetermined number of myotomes and a consequent breaking up of the regular metamerism of the axial muscles.

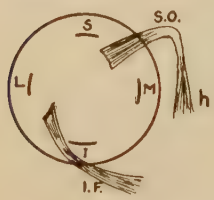


Fig. 528.—Eye muscles as seen from behind. *s.o.*, superior oblique, the posterior belly of which, *h*, runs in a plane at right angles to the page; *I.F.*, inferior oblique; *I.L.M.S*, points of attachment for the inferior, lateral, median, and superior rectus muscles respectively. (After Weber.)

1. Head

Skull muscles are few in number, being reduced in correlation with the increasing absence of movable skeletal parts in this region. The three anterior pairs of myotomes become the muscles that move the eyeballs within their sockets, but as these muscles are conservative, they exhibit only minor modifications throughout the vertebrate series. There are six pairs of them (Fig. 528), the most anterior identifiable myotome (Fig. 527), which is supplied by the third cranial nerve (oculomotor) giving rise to the *superior rectus*, the *internal* or *medial rectus*, the *inferior rectus*, and the *inferior oblique muscles*. The myotome next posterior, which is supplied by the fourth cranial nerve (trochlear), becomes the *superior oblique muscle*, and is followed, after a gap that probably represents a missing myotome, by one supplied by the sixth cranial nerve (abducens), which is responsible for the

external or *lateral rectus muscle*, and the *retractor bulbi*, which latter first appears in amphibians.

Included also among the derivatives of the myotomes of the head, in all vertebrates except fishes, are the muscles supplied by the twelfth cranial nerve (hypoglossus). This nerve with its muscle segments, which have to do with the tongue (Fig. 529), probably represents the fusion of several neuro-muscular units that have been incorporated into the head from the metameric vertebral series at the anterior end of the body. In most vertebrates these muscles, namely, the *hyoglossal*, *styloglossal*, and *geniohyal*, are extrinsic, that is, not forming a part of the tongue itself, but in mammals there is an additional muscle, the intrinsic *lingualis*, which makes up the bulk of the fleshy tongue.

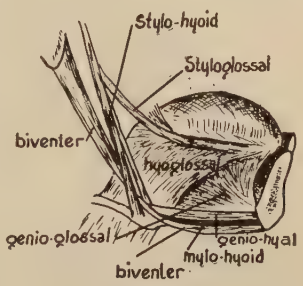


FIG. 529.—Muscles of the human tongue. (After Gegenbaur.)

2. Trunk

In cyclostomes, which are without a definite lateral line, the muscles of the trunk and tail are undifferentiated, but in fishes as a rule they are divided into dorsal and ventral regions by the *lateral line*, being supplied respectively by the dorsal and ventral branches of the spinal nerves. These two general muscular areas are destined to undergo different fates with further evolution and development.

a. VENTRAL

In urodeles the *ventral trunk musculature* becomes delaminated into four sheets of muscle with the gradual obliteration of the myocommata that separate the myomeres from each other. Along the mid-ventral line on both sides of the linea alba, the muscle fibers still retain their original longitudinal arrangement, and together form a flat band of muscle, the *rectus abdominis*. On the sides, however, the body wall is composed of three layers, with the fibers of each layer assuming different directions. Next the peritoneum, the innermost layer, or *transversus abdominis muscle*, has the fibers tending to run around the body at right angles to the long axis. Outside the transversus are two diago-

nal layers, the *internal* and *external oblique muscles*, having fibers at right angles to each other (Fig. 530).

In all such reptiles as lizards and alligators, the ventral axial muscles are still further modified by the introduction of en-

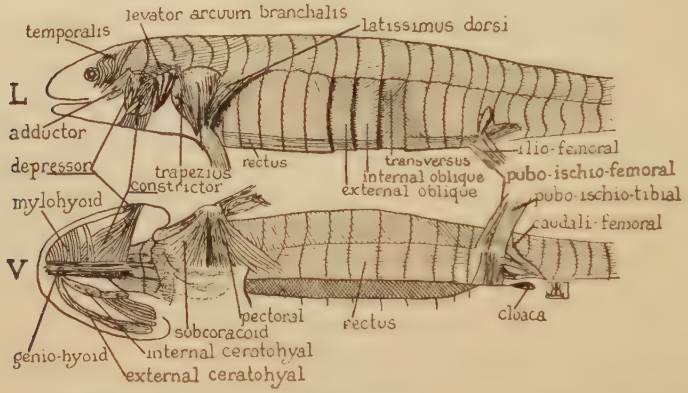


FIG. 530.—The musculature of a salamander. *L*, lateral; *V*, ventral. (After Bütschli.)

circling ribs in the anterior part of the body region. Posteriorly in the region of the belly the original layers of muscles remain, but anteriorly the oblique muscles become broken up into the

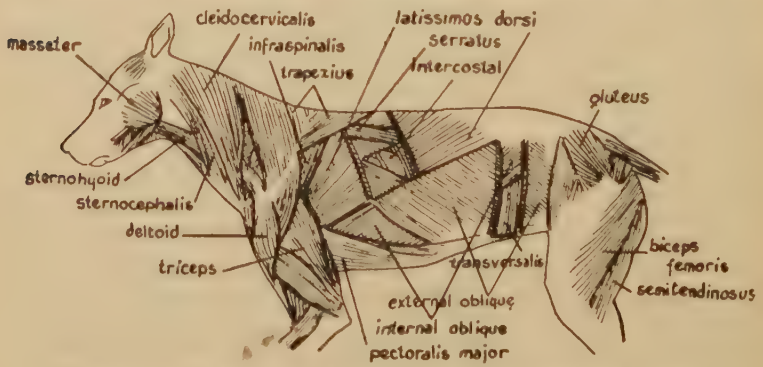


FIG. 531.—The muscles of a dog. (After Ellenberger and Baum.)

external and *internal intercostal muscles*, which extend from rib to rib and aid in respiratory movements. In the neck region in front of the ribs the oblique layers furnish material for the *scalenus muscles*.

Among birds the oblique muscles are poorly developed, the transversus is absent, and the rectus abdominis is reduced in size and is posteriorly unsegmented. This sacrifice of the ventral axial muscles is compensated, however, by an excessive elaboration of the appendicular muscles of flight.

The oblique muscles in mammals give rise both to the intercostals and the *serratus muscles*, which come to assume more of a dorsal than ventral position, although still supplied from the ventral branch of the spinal nerves (Fig. 531). Other mammalian muscles of ventral axial origin are the *psoas muscles* of the posterior abdominal wall, and the *colli muscles* of the neck region.

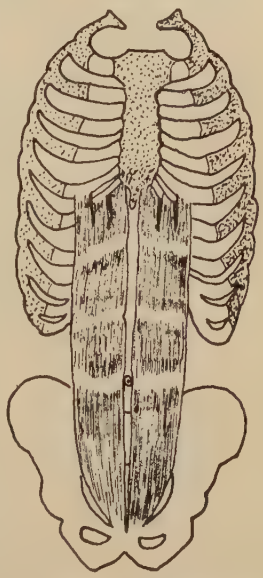


Fig. 532.—The *rectus abdominis* muscles in man, showing the transverse *inscriptiones tendiniæ*. (After Mollier.)

Furthermore, in reptiles the rectus abdominis muscle loses its primitive character by the introduction of the sternum, so that it becomes broken up into presternal and poststernal parts. Some of the presternal muscles are the *sternohyoid*, *sternothyreoid*, and *thyreohyoid* of the neck region. The poststernal part retains somewhat more of its primitive character, even as far up as mammals, where traces of the myocommata, in the form of the *inscriptiones tendiniæ*, may still be seen as transverse interruptions of the broad flat rectus muscle. These depressions of connective tissue are represented by sculptors of classical times on the abdomens of many Greek statues, which is curious incidental evidence of the retention on man till comparatively recent times, of these telltale ancestral marks (Fig. 532).

The myomeres of the tail region are of great importance to fishes, enabling them to swim. They are little modified, because the lateral movements of the tail are not complicated and are best accomplished by primitive metameric myomeres. In higher forms the caudal myomeres lose their original significance and become modified into reduced muscles sufficient to control varied tail movements in such land animals as sport a caudal

appendage, while in the anal region some of the myomeres become entirely freed from skeletal connection and are transformed into *sphincter muscles.*

b. DORSAL

The *dorsal-axial musculature* differentiates more slowly, but eventually, with the development of the vertebral processes offering places of attachment, it gives rise to a greater array of separate muscles than is found below the lateral line. In the consideration of these dorsal-axial muscles care must be taken to avoid confusion with the appendicular muscles with which they are intimately involved.

Fishes and urodeles show little differentiation of dorsal-axial muscles, but reptiles have gone far enough in the elaboration of the neural arch of the vertebral column and its processes to give foothold to a large number of small muscles that, with their tendons, tie together the different vertebræ.

The longest dorsal muscle is the *longissimus dorsi*, which extends lengthwise between the neural spines and the transverse processes. Groups of shorter muscles, metamerically arranged, extend (1) from one transverse process to another, *intertransversarii;* (2) from the neural spine of one vertebra to the transverse process of the one in front of it, *transversospinales;* (3) from the transverse processes to the ribs, *transversocostales;* and (4) from one spine to another, *interspinales.*

In birds the dorsal muscles of the rigid thoracic area are largely atrophied, except in the neck region where they are very much elaborated, as anyone who has faithfully wrestled at the dinner table with the neck of a chicken, can easily testify.

The dorsal-axial muscles of mammals are more like those of reptiles than of birds, but are influenced more than in either of these groups by the appendicular musculature which increases much in importance.

3. Diaphragm

The dome-shaped muscular diaphragm comes from ventral axial elements in the neck region, and after gradual displacement assumes a transverse position across the bottom of the thoracic basket (Fig. 348). It is pierced by the esophagus and by large arterial and venous trunks, as well as by the tenth pair of cranial nerves (vagus) and the sympathetic trunk. Its own nerve

supply, as already stated, comes from the cervical region in the form of the *phrenic nerve.*

The *transverse septum,* which separates the pericardial from the body cavity in the lower forms, is probably not homologous except in part with the muscular diaphragm in mammals.

B. Appendicular Muscles

The muscles of the appendages are derived from the myotomes of the axial musculature. In the case of elasmobranch fishes, for example, at the region where the pectoral and pelvic fins are to become established, the ventral buds of the lateral myomeres sprout out *myotomic buds,* two for each myomere (Fig. 533). These become the fin muscles. Not only do the myomeres exactly opposite the future fin produce buds, but several others immediately anterior and posterior to these also crowd together, adding contributions. The result is that a generous number of muscular elements take part in the formation of the fin musculature, and the accompanying nerve supply is enough to form a plexus of nerves which adequately insures the future performance of the fins.

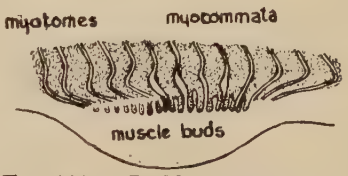


Fig. 533. — Budding muscles of appendage, from myotomes in *Pristiurus.* (After Rabl.)

In general the locomotor muscles may be classified into two groups, extrinsic and intrinsic, although the distinction is not always unmistakable.

1. Extrinsic Muscles

Extrinsic muscles are those of the girdles and proximal ends of the appendages. They connect the appendages with the axial skeleton and move the limbs as a whole. *Intrinsic muscles,* on the other hand, have both origin and insertion within the appendages, only effecting movements in parts of them.

In fishes the extrinsic group is most in evidence, consisting of *elevators* and *depressors,* which lift and lower, and *abductors* and *adductors,* which spread and contract skeletal parts. All of these muscles move the fin as a whole. Since there is little occasion, in the performance of mass movements useful in a water medium, for the niceties of movement effected by intrinsic muscles, these are absent. With the establishment of systems of appendicular

levers in connection with land life, however, there is an increase of intrinsic musculature, and *rotators*, which rotate, and *extensors* and *flexors* which straighten and bend, are added, as well as *pronators*, or in-twisters, and *supinators*, or out-twisters.

The extrinsic muscles of the pectoral appendages are better developed than those of the pelvic appendages, owing to the difference in the attachment of the respective girdles to the axial skeleton. The pelvic appendages are anchored securely to the backbone and so require fewer intermediary muscles than the pectoral appendages, which are often entirely unattached by direct skeletal elements.

In the pectoral appendages, particularly of birds, the extrinsic muscles reach a high degree of development, being packed largely on either side of the keeled sternum, and quite covering over and obscuring the axial muscles. The muscles of flight (*pectoralis*), in a pigeon may equal as much as one-fifth of the entire body weight.

2. Intrinsic Muscles

The intrinsic muscles of the appendages in primates, including man, are more primitive than in many other vertebrates. This is because the generalized pentadactyl skeletal framework is still retained in primates, while in many other forms there is a reduction of distal skeletal parts, and a consequent modification of the musculature. The generalized pentadactyl appendages of man constitute one of the factors contributing to his dominance. More possible avenues of diversified activity are by this means left open, than when extreme specialization takes place, as in the leg of a horse, the flipper of a seal, or the wing of a bird.

Birds exhibit a curious modification of intrinsic muscles and tendons in the *perching mechanism*, whereby they are enabled to go to sleep upon a branch without falling off. The muscles which flex the toes are located high up on the leg so that they will not interfere with the bending of the joints, and the long tendons extend to the tips of the toes where they are inserted. Whenever a bird settles to roost, the tendons pull the toes shut because the weight of the body folds up the skeletal levers of the legs, and the resulting stretching of the tendon, as it passes over the metatarsal joint (Fig. 518), automatically closes the toes. They remain closed as long as the weight of the body keeps the tendons taut. In order to release the grasp upon the perch the bird must "stand up," and so relax the pull on the tendons.

2. Branchiomeric Muscles

The muscles of the splanchnocranium are derived from that part of the mesoderm which remains ventrally after the dorsal myotomes have been established. They are associated with skeletal parts representing a "boom that failed," in the evolutionary sense. Consequently they undergo many makeshifts with the disappearance or modification of their original skeletal connections.

The branchiomeric muscles are most apparent in elasmobranch fishes, where four groups, according to the nerve supply, may be clearly distinguished, namely: the trigeminal, facialis, glossopharyngeal, and vagus.

To the first group, supplied by the mandibular branch of the trigeminal nerve (V), belong the muscles of the mandibular arch of the splanchnocranium, or the primary jaws. These include the muscles of mastication, such as the *temporalis* and *masseter*, in the higher forms. The small *tensor tympani* muscle of the middle ear in mammals is a derivative of one of the muscles of the mandibular group.

In the second group are the muscles of the hyoid arch, for example, the *stylohyoid*, that are supplied by a branch of the facialis nerve (VII). A transformed muscle of this group in mammals is the tiny *stapedius*, which extends from the stapes to the wall of the tympanic cavity, and is probably the smallest muscle of the vertebrate body with a definite individuality of its own.

The third group has to do with the tongue, and muscles included in it are supplied by the glossopharyngeal nerve (IX), while the last group, supplied by the vagus nerve (X), includes muscles that spread and close the gill arches, so long as these remain. In higher forms, when the spinal accessory nerve (XI) becomes admitted to the group of cranial nerves, the two together provide for the *trapezius*, between head and neck, and the *sternocleidomastoid muscles* that extend between the shoulder and neck.

3. Integumental Muscles

The integumental, or dermal, muscles are split off embryologically from the underlying skeletal muscles, and while in many cases retaining their skeletal origins at one end and inserting under

the skin at the other, they sometimes, as in sphincter muscles, lose all skeletal connection.

The tight-skinned fishes are without any dermal musculature, while amphibians have only a trace of anything of the kind in the tiny muscles that open and close the lids of the nostrils.

Snakes, among reptiles, use integumental muscles for locomotion, for these enable the scales to get a grip on the substratum. This can be easily demonstrated by placing an active snake upon a level sheet of glass and observing the difficulty it encounters when the dermal muscles are thus made ineffective on a surface that cannot be gripped by scales.

Birds fluff the feathers by means of integumental muscles, in this way changing the thickness of the layer of warmed air held

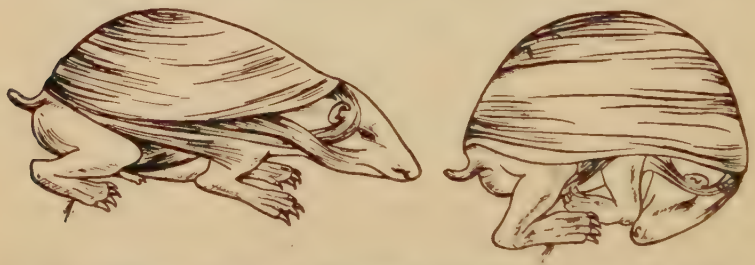


FIG. 534.—European hedgehog, *Erinaceus*, with the skin removed, showing the manner in which it rolls up by contraction of the integumental musculature. (After Nuhn.)

next the body, which regulates the body temperature. The so-called *patigial muscles* in the web of a bird's wing that assist in flight, belong to the integumentary group, but are derived from the pectoralis muscles of the breast, and various muscles of the shoulder and arm.

It is in mammals, however, that integumentary muscles reach their greatest differentiation, serving a wide range of uses from defense to the expression of the emotions.

Under *defensive skin muscles* may be mentioned (1) those which cause hairs and bristles to stand on end in terrifying fashion, as on the tail of a frightened cat, or on the scruff of an angry dog's back; (2) those which erect defensive spines or quills, as in the skin of the "fretful porcupine," *Erethizon*; (3) those which enable the animals, like armadillos, and the European hedgehog, *Erinaceus* (Fig. 534) to roll up into an impregnable ball; and (4) muscles

which tend to dislodge annoying insects by causing the skin to shudder or twitch, as on the neck, shoulders, and anterior region of a horse's sides, but which are less evident on the hips and flanks within reach of the swishing tail (Fig. 535).

Integumental muscles play a rôle in the *expression of the emotions*, particularly in man. Generally speaking, there is no visible expression of the emotions by dermal muscles in the lower animals. The "state of mind," whether it be fear, anger, or excitement from any cause whatsoever, is usually shown by movements and attitudes of the body, rather than by the action of the skin muscles of the face. Most animals have a "poker face," which does not reveal anything that may be mentally happening behind the facial mask. Whatever expression shows is usually centered in the eyes. In the rigid face of a fowl, for instance, the lively eye gleams like a jewel.

Fig. 535.—The integumental muscles of a horse, by means of which the skin may be "shuddered" for dislodging annoying insects. These muscles are absent on the flanks, which can be reached by the swishing tail. (After Nuhn.)

Among carnivorous animals and the primates, however, the dermal muscles of the face take on character, until in man it is the evanescent expression wrought by the facial muscles, so difficult to analyze and to secure by the artist, that remains in the memory long after the form of the body is forgotten. The facial muscles that are most expressive in man and least developed in brutes, are those at the inner extremities of the eyebrows and at the angles of the mouth.

Integumentary muscles fall into two general groups, according to their derivation, first, the *panniculus carnosus* group, from the *latissimus dorsi* and *pectoralis* muscles, and second, the *sphincter colli* group, from the branchiomeric musculature of the hyoid region, under the dominance of the seventh pair of cranial nerves.

The *panniculus carnosus* is particularly evident in mammals, although traces of it occur in the lower vertebrates. It is a thin sheetlike muscle that tends to wrap about the body under the skin. In monotremes it extends as far as the cloaca, and includes

a *sphincter marsupii*, and a *sphincter cloacæ*. In the rorqual, *Balænoptera*, it likewise extends from mouth to anus, while in the right whale, *Balæna*, it is confined to the head region.

Fragments of the panniculus carnosus remain longest in the axillary, inguinal, and sternal regions. These fragments make up the shuddering muscles of the horse, already referred to, and the muscles by means of which a wet dog shakes itself. There is

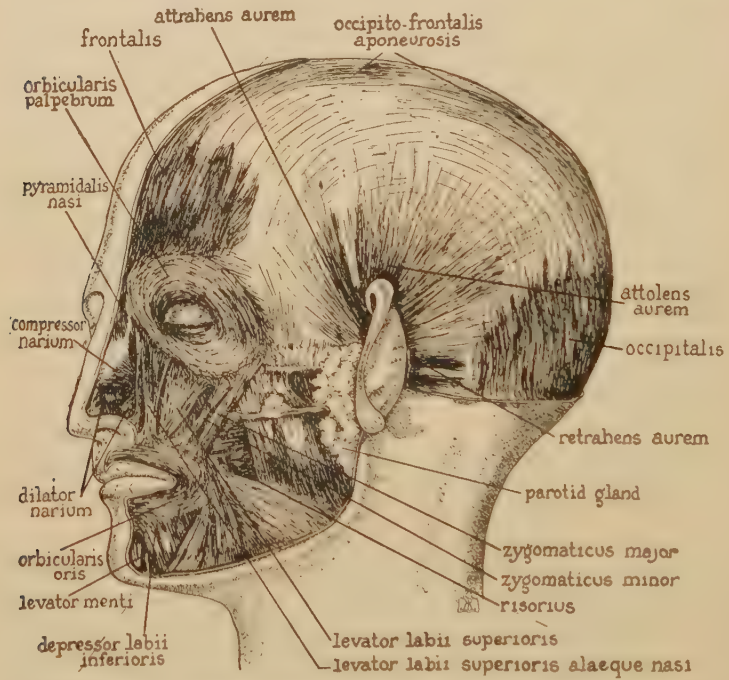


Fig. 536.—Muscles of facial expression in man. (After Deaver.)

also an occasional *sternalis* muscle under the skin outside the pectoralis, which is sometimes visible in man when well enough developed.

The *sphincter colli* group of muscles, originally associated with the hyoid arch, is supplied by the facialis nerves (VII). During its evolution it migrates and expands so as to spread over the head and down on to the shoulders, eventually becoming differentiated into a superficial sheet of muscle that is designated as the *platysma* and the sphincter colli proper, according to its location.

With the upgrowth of the cranium that part of the platysma extending over it becomes divided into an occipital and a facial part, separated by a broad sheet of connective tissue, the *galea aponeurotica*, which stretches over the top of the cranium. The facial parts of the platysma may be classified into four groups of superficial muscles, in close association with the underlying muscles of mastication, which are the muscles of the external ear, eyebrow, nostril, and of the lips and cheeks (Fig. 536).

The *muscles of the ear*, namely, the *auriculares anterior, posterior*, and *superior*, enable an animal to turn the pinna of the external ear toward the source of a sound without changing the position of the head. They are better developed in animals like horses and dogs than in man, although fragments still remain in some individuals, enabling them to "wiggle the ears."

Fig. 537.—The shedding of tears involves several facial muscles of expression. (From the Journal of Heredity.)

The *eyebrow* group takes in four muscles, the *orbitofrontalis;* the *orbicularis oculi;* the *levator palpebræ superioris;* and the *corrugator supercilii* or brow wrinkler. The eyebrow has been well described as "the rainbow of peace or the bended bow of discord."

Three more or less well developed muscles of the *nostril* group are the *levator labii superioris et alæ nasi*, by means of which man and beast sneers and snarls; the *depressor nasi;* and the *compressor nasi*, which draws down or compresses respectively the wings of the nose.

Finally, the *lips and cheek* group, consists of a strong *sphincter* muscle, the *orbicularis oris*, around the mouth opening, from which radiate several muscles. Of these the *risorius muscle*, attached at the angles of the mouth opening and pulling in opposite directions laterally, and the *triangularis*, pulling down the corners of the mouth, serve in human beings to express the diverse emotions of laughter and tears (Fig. 537).

The deeper-lying remains of the *sphincter colli proper* are well developed as muscles enwrapping the neck in such animals as turtles and birds, and are present in some degree even in man.

Finally, of the facial muscles of expression, those of the ear group may be regarded as *regressive*, having disappeared entirely in a considerable percentage of mankind, while the "psychological muscles" of the face, that accompany increasing intelligence and reach their greatest differentiation in man, are *progressive* muscles, the evolution of which is by no means completed.

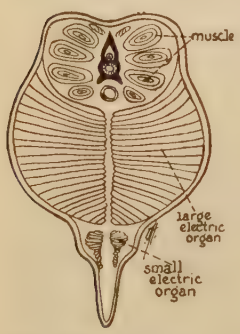


FIG. 538. — Electric organ of the electric eel, *Gymnotus*. (After Haller.)

VI. ELECTRIC ORGANS IN FISHES

In a few exceptional elasmobranchs and teleosts, for example, the electric ray, *Torpedo*, the electric eel, *Gymnotus* (Fig. 538), the star-gazer, *Astroscopus*, and the African *Malapterurus*, certain muscles have become transformed into electric organs which can deliver a shock, more or less profound, to animals that disturb them.

Structurally an electric organ consists of a number of regularly arranged elements, called *electroplaxes*, put together in histological layers, nervous, striated, and nutritive, that remind one of the plates in a storage battery. It is not difficult to imagine how these structures have developed from muscles, since normally muscles in action discharge a certain amount of electricity. The fact that the mechanism, although developed in different parts of the body in different species, is always derived from muscle tissue, indicates that it is a physiological adaptation and not a morphological inheritance of one form from another.

CHAPTER XIX

THE DOMINATING FACTOR (NERVOUS SYSTEM)

I. GENERAL CHARACTER

It is customary to arrange animals in an ascending scale according to the degree to which the nervous system is developed, for no other part of the body plays so large a rôle in determining "the place in the sun" which any competitive organism comes to hold.

Plants, although entirely lacking a nervous system as commonly understood by that term, nevertheless may be intimately and successfully related to their surroundings. The multitudinous impressions from without that constantly bombard living things, however, are transmuted into more apparent and stirring responses by animals than by plants.

The nervous system is a conducting apparatus that receives sights, sounds, and other physical, as well as chemical contacts with an ever changing environment and hands them on to centers of judgment and adjustment within the organism itself, which, aided by further conducting mechanisms in turn, bring about action.

In higher animals, such as man, the nervous apparatus becomes the seat of intelligence, the storehouse of memory, and the headquarters of the affections and the will, while in the less endowed so-called "lower animals," the beginnings of these desirable acquisitions already appear.

The important dominating nervous mechanism is for the most part out of sight and quite secondary to the skeletal framework, musculature, and visceral parts in determining the general contour of the body, yet, if by some magical technique the entire body substance, except the ubiquitous nervous apparatus with all its ramifications, could be harmlessly spirited away, there would still remain in place a gauzy fabric of innumerable spidery cells and finespun fibers, that would preserve completely in ghostlike form the original outlines of the body.

The great importance of the nervous system is shown inasmuch

as it is laid down very early in embryonic development and outstrips all other groups of tissues during the first rush of embryonic growth. As Wiedersheim has pointed out, it presents comparatively few rudimentary or degenerate structures.

Fortunately the whole intricate nervous mechanism, consisting as it does of stimulus-receiving devices of various kinds, transmission cables and meshworks, and ganglionic masses, together with accessory supporting and protective parts, may be resolved into component units, both structural and functional, and thus rendered intelligible. The structural units are modified cells by means of which the functional units, or reflex arcs, are made possible.

II. THE STRUCTURAL UNITS

As would naturally be expected, the ectoderm, that is, the embryonic tissue that presents primary contact with the environment, gives rise to the principal cells destined to form the nervous system. These ectodermal cells depart very far from their original epithelial compactness, and become either true nerve cells (*neurones*), or non-nervous structures (*neuroglia cells*), which have a secondary supportive or skeletal rôle. Other cells, coming from the embryonic mesoderm, may also serve the all-important neurones in the form either of nutritive blood vessels or of protective sheaths.

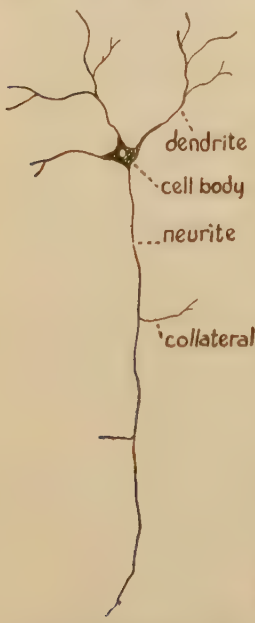


Fig. 539.—A nerve cell.

Neurones, after differentiation, vary enormously in size and shape but all bear a common family resemblance to each other. The cell body surrounding the nucleus sprouts out into various processes, the so-called "nerve fibers," that may become enormously lengthened and attenuated (Fig. 539), but always remain an essential part of the cell under the immediate control of the nucleus. Thus the nerve cell assumes a form well adapted to its primary function of transmission at the same time that it is specializing in sensitivity, a function which is simply one of the general endowments common to all cells.

By "joining hands" these long-drawn-out neurones form continuous living bridges and networks that connect points of stimulation with points of reaction. They are, therefore, conductors which, like telegraph wires, permit the passage of messages while remaining stationary themselves.

This capacity of conduction results in a polarity, or one-way traffic, within neurones. Impulses enter neurones along certain fibers and depart by others, a relation which is never reversed. The fibers forming incurrent pathways with respect to the cell bodies are known as *dendrites*, because they present abundant treelike arborizations. The excurrent pathway, on the other hand, is through a special fiber called the *neurite*, which is usually larger and longer than the more numerous dendrites, and not so much given to branching. Whenever branching does occur in a neurite, the twigs, or *collaterals*, characteristically leave the main fiber at right angles, except at the tip of the neurite, instead of by acute angles as in the dendrites (Fig. 539). The neurites of certain nerve cells in man may reach an actual length of two feet, an astonishing span for any single animal cell unit to attain. The end of such a neurite is thus frequently nearer the nucleus of some neighboring cell with which it may be in touch, than its own nucleus.

FIG. 540.—Stages in the transformation of a bipolar neurone into an apparently unipolar neurone.

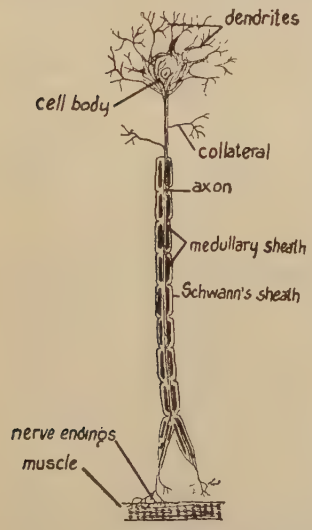


FIG. 541.—Diagram of a multipolar neurone, with sheaths. (After Plate.)

The actual contact between the neurite of one neurone and the dendrite of another, results in a physiological continuity, termed a *synapse*, but synapses are not established until the embryonic neurones (*neuroblasts*) have sprouted out their cell processes sufficiently to make contact possible. Thus, the pathways that characterize the nervous system, are gradually and secondarily established.

Neurones may be *bipolar* or *multipolar*, according to the type of polarity which they exhibit. The bipolar type, with one centripetal dendrite and one centrifugal neurite, is the more primitive of the two types. Multipolar neurones usually have several dendrites and a single neurite. An apparently *unipolar* type, such as occurs in the dorsal ganglia of the spinal nerves, results when the basal ends of a neurite and a dendrite join for a short distance upon emerging from the cell body. In reality, however, this is a bipolar cell that has secondarily taken on a unipolar aspect as a result of the mechanics of growth (Fig. 540).

When a neurite ends in a muscle fiber or a gland it may enlarge either into a flattened *end plate*, or bulb, or expand into a tiny brush, or end simply like a thread. The distal tips of neurites and dendrites, at the points of synapses, form the weakest link in the chain of neuronic elements.

There are at least four categories of nerve fibers, as follows:

1. Naked processes (*axons*) without sheaths, occurring in the gray substance of the central nervous system, and in some of the nerves of the sympathetic nervous system.
2. Axons with a protective sheath (*Schwann's sheath*), occurring in invertebrate "nerves" generally, in amphioxus and the cyclostomes, in olfactory nerves, and at the distal ends of spinal nerves where they enter an effector apparatus.
3. Axons with an insulating sheath of fatty tissue (*medullary sheath*), occurring in the white substance of the central nervous system.
4. Axons with both sheaths present, the medullary sheath inside and Schwann's sheath outside, occurring in nerves generally except at the ends.

All of these types of sheaths are diagrammatically represented upon a single neurone in Fig. 541.

III. REFLEX ARCS

The functional units of the nervous system are *reflex arcs*, which involve two or more neurones, and at least five functional elements in each case, namely: (1) receptor; (2) sensory transmitter; (3) adjustor; (4) motor transmitter; and (5) effector (Fig. 542). The last element is usually not a part of a motor neurone but is a muscle or a gland with which it is in connection (Fig. 543). Re-

ceptors, usually more numerous than effectors, may be composed in part of accessory non-nervous elements, which, though serving as the terminal links in a sense organ, are outside the neurones themselves.

Accordingly the reflex arc should not be regarded solely as a nervous apparatus, but rather as a neuromuscular, or neuroglandular, mechanism.

A reflex arc may be almost indefinitely enlarged and extended by the insertion of additional so-called *internuncial neurones*, serving as *relayers*. In fact, a large part of both nerve cord and brain is made up of such intermediate neurones, which increase the distance in the chain between receptors and effectors, making complex relationships not only possible but inevitable.

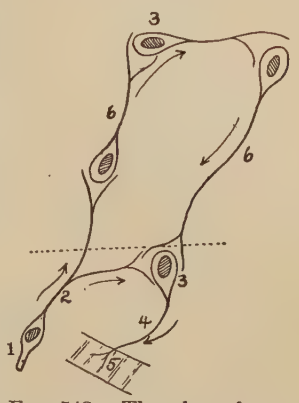


FIG. 542.—The plan of a reflex arc. *1*, receptor; *2*, sensory transmitter; *3*, adjustor; *4*, effector transmitter; *5*, effector; *6*, relayer. Below the dotted line is represented a simple reflex; above, a more complicated reflex involving more neurones.

Many reflexes, such as those resulting in respiration and the secretion of digestive juices, are quite automatic and predictable, and involve only the cord and not the brain, with the exciting stimulus usually coming from within. Others "go around Robin Hood's barn" through the adjusting centers of the brain, often resulting in conscious behavior.

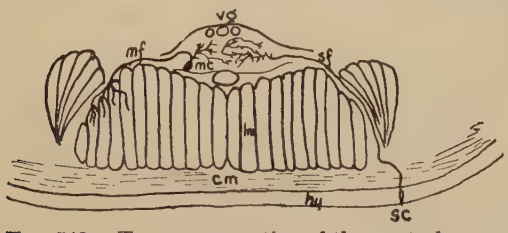


FIG. 543.—Transverse section of the ventral nerve chain and surrounding structures of an earthworm. *cm*, circular muscles; *hy*, hypodermis; *lm*, longitudinal muscles; *mc*, motor cell body; *mf*, motor nerve fiber; *sc*, sense cell; *sf*, sensory fiber; *vg*, ventral ganglion. (After Parker.)

Holmes defines *habit* as "action in the present from motives in the past." Consciousness, which may have been conspicuously present in the first stages of habit formation, fades eventually into the background, so that habit-action comes secondarily to assume a resemblance to automatic unconscious reflexes.

Memory and learning are built up out of *conditioned reflexes*,

as a result of reflex arcs that involve detours of sensory impressions and motor responses, passing through adjustment centers not located on the primary highway. For example, anyone who has once viewed a skunk and experienced its compelling odor, has only to receive again the visual stimulus produced by seeing this conspicuous black and white creature, in order to recall vividly the accompanying odor, even though the odor be absent. The natural response of retreat at the sight of this jaunty self-confident animal is not a direct reaction to its color and form, but instead to a possible disagreeable odor associated with the visual impression that it makes.

IV. EVOLUTION OF THE NERVOUS SYSTEM

The complex human nervous system was a long while being developed. In a simple animal, like an *Ameba*, the whole body is a single cell mass of protoplasm, possessing a generalized capacity for irritability and contractility. Whenever a stimulus impinges at some spot upon such a body there results a direct response at the point of stimulation, but the news of it travels slowly, if at all, to other parts of the cell, although the fact that an *Ameba* in escaping from danger will extrude a pseudopod on the side opposite to a point of stimulation, is an indication that some degree of protoplasmic conduction exists even here. It is out of the question in such a case, however, to speak of sense organs or receptors, of communicating nerves, of adjusting centers, or of reacting muscles, because they are absent.

Probably the first step towards any real neuromuscular mechanism comes, as pointed out by Parker, in the group of the sponges in which certain somewhat modified cells, *porocytes*, which surround the pores leading into the watery highways that penetrate these lowliest of cell aggregates, contract upon suitable stimulation to close the pores. There is, however, no nervous receptor present to receive the stimulus. The porocyte itself, like the part of an *Ameba* which is exposed to local stimulation, contracts directly when stimulated, without the mediation of any separate sensory receptor. Thus, the "muscle" element becomes active before the "nervous" element.

FIG. 544.—Diagram of an independent effector. A muscle cell, such as occurs in the lowest multicellular animals. (After Parker.)

The same thing happens in the embryonic stages of higher forms of life, as, for instance, when the heart begins to beat before its nerve supply has been established. This preliminary stage is called by Parker, who has admirably worked out the early steps of nervous development, the *independent-effector stage* (Fig. 544).

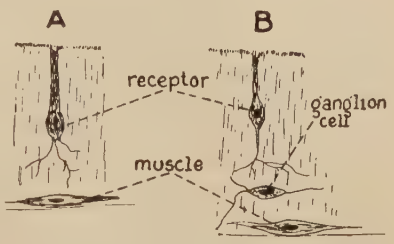


Fig. 545.—Diagram of receptor-effector systems, such as is seen in sea anemones. *A*, simple type; *B*, more complex type with the insertion of a ganglion cell. (After Parker.)

The real beginning of a complete neuromuscular mechanism, however, comes later, when a sensory cell, or unit, transfers a stimulus received to some reacting cell with which it is in contact. Such an advance may be termed the *receptor-effector stage* (Fig. 545, A). In its most primitive form it is exemplified in the Cœlenterates, for example, *Hydra* and sea anemones, where specialized ectodermal cells exposed to the outside, communicate the stimuli which they receive directly to a contractile inner part of the stimulated cells or to neighboring contractile cells within.

The next step comes with the formation from the receptor-effector units, of *diffuse networks* between the two types of cells (Fig. 546). By this means stimuli impinging upon a few receptors may be distributed to many effectors, and thus the result becomes magnified and rendered more efficient. These diffuse networks, which occur in such animals as jellyfishes, do not constitute a true central nervous system, since they are not typically composed of independent synaptic neurones, having dendrites and neurites through which impulses travel with definite polarity.

Fig. 546.—Nerve network from a small blood vessel in the palate of a frog. (After Prentiss.)

In some Cœlenterates particularly, a continuous nerve net is found lying between receptors and effectors. For the units of this nerve net Parker proposes the name of *protoneurones* (Fig. 547, A). These are perhaps the forerunners of the internuncial cells which later are to form the bulk of the central nervous system. With the addition of central elements that bring

about adjustment and modification between receptor and effector, the *adjustor stage* is reached (Fig. 545, B).

The central adjustor elements originate on the outside and come to assume their protected inside position by inward migration. It follows that when they are thus cut off from the outside world they are helpless by themselves without the mediation of sensory receptors which will bring them again into communication with the stimuli of the environment. In other words, the establishment of a central adjustor

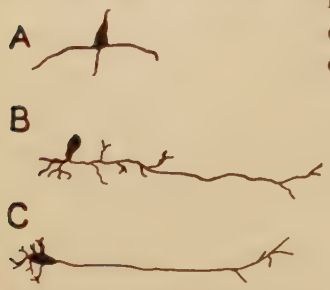


FIG. 547.—Evolution of a motor neurone. *A*, protoneurone, from the nerve net of a cœlenterate; *B*, neurone from an earthworm; *C*, primary motor neurone of a vertebrate. In all cases the receptor end is at the left and the discharging end at the right. (After Parker.)

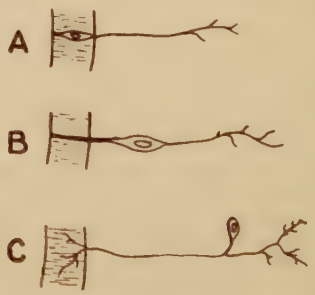


FIG. 548.—Evolution of sensory neurones. The cell body becomes more and more withdrawn from the surface. (After Parker.)

system necessitates the elaboration of special sense organs in order to bring the central system into outside communication. The evolution of motor and sensory neurones is shown in Figs. 547 and 548.

In invertebrates generally, the inward migration of the central nervous system comes about through a splitting off of the thickened epidermal cell mass by delamination (Fig. 3, B). All stages of this process are found in the formation of the nerve cord of different species of annelid worms. In *Sigalion*, for example, the entire central nervous system remains in intimate connection with the body wall in the form of an internal ridge of ectodermal cells. In *Nereis* the main part of the cord is split off while the anterior end, or "brain," is still fused with the internal body wall, while in the earthworm, *Lumbricus*, both cord and brain lie within the body, entirely detached from the outside ectoderm.

During the establishment of the central nervous system in

worms, the ectodermal cells forming it, which by delamination retreat from external exposure, retain in general their original external position with reference to the outside world, that is, the cell bodies with their nuclei face outward toward the source of stimulation, while the cell fibers extend inward to connect with the effectors.

In vertebrates, on the contrary, with the exception of the cyclostomes and some fishes, the central nervous system is typically buried by a process of *invagination* (Fig. 3, A), whereby cells originally facing outward come to face inward toward the central canal, with their tail-like processes radiating outward. As a result of this reversal it is all the more necessary for these invaginated cells which, in becoming centralized, have literally turned their backs upon the outside world, to attain communication by means of synapses, not only with the receptors without but also with the effectors within. So the rise of the adjustor, or central mechanism in the reflex arc, comes about and the morphological way is opened for the vast and intricate development necessary in the attainment of the intellectual life.

Finally, centralization is followed by *cephalization*, or the concentration, literally, into "headquarters" of the central mechanism.

The six high points in the evolutionary emergence of the nervous system from *Ameba* to man are: (1) local-response stage without correlation; (2) independent-effector stage; (3) receptor-effector stage; (4) diffuse-network stage; (5) adjustor stage; (6) cephalization stage.

V. EMBRYONIC FORMATION OF THE NERVOUS SYSTEM IN VERTEBRATES

The first step in the formation of the vertebrate nervous system occurs towards the end of the gastrula stage of development, when the ectoderm in front of the blastoporic lip thickens to form the neural, or *medullary plate*, which extends lengthwise along the dorsal side of the elongated embryo. This structure is continuous and, since the embryonic ectoderm is not conspicuously given to metameric expression, it is never marked off into segments, as is the mesoderm in the formation of the somites.

Next, the lateral edges of the long medullary plate become

elevated, thus transforming it into a troughlike canal, the *medullary groove* (Fig. 114). These edges continue to grow upward until they eventually meet and grow together to form the *medullary tube.*

Finally, the closure of the tube begins in the middle region and extends both ways, so that for a time both ends remain open. At the posterior end there may exist, in addition to the troughlike opening to the outside, a temporary inward passage-way around through the blastopore into the primitive enteric cavity (Fig. 116). This is the *neurenteric canal.* In man the medullary groove begins to close about the fifteenth day, while the neurenteric canal has entirely disappeared a week later. The anterior end of the medullary groove remains unclosed longer than the posterior end in the form of the so-called *neuropore.* Amphioxus retains this opening throughout life (Fig. 214), and it may serve as some sort of a sense organ in this forerunner of the vertebrates, but in man it closes about the fourth week.

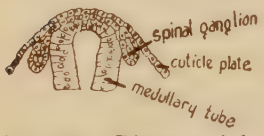


FIG. 549.—Diagram of the neural crests which form the spinal ganglia. (After Piersol.)

The medullary tube is at first comparatively straight, but soon assumes somewhat the shape of a question mark, due to the rapid growth of the incipient brain at its anterior end.

As the medullary tube closes, there form on either side along the line of fusion two ridges of medullary tissue, the *neural crests* (Fig. 549). At first continuous with the tube, these later gain independence through the insertion of growing mesenchymal tissue between them and the tube. Eventually they break up into chains forming the *spinal ganglia* and the sympathetic system, whose sprouting neurones gain secondary connection with the cord. In this manner all the nervous tissues of the body are derived, either directly or indirectly, from the medullary tube, with the exception of the cells and fibers of the olfactory epithelium.

In many teleosts the *anlage* or foundation of the spinal cord is formed first into a solid rod, which afterwards becomes hollow (H. E. Ziegler).

VI. THE CORD

For clarity of description the parts of the nervous system will be arranged in the following order:

I. Central nervous system.
   1. Cord
   2. Brain
II. Peripheral nervous system.
   1. Spinal nerves
   2. Cranial nerves
III. Involuntary nervous system.
IV. Sense organs (Chapter XX).

1. Form of the Cord

The human nerve cord may well be used as a basis for description not only because it is of more immediate interest than that of other vertebrates, but also because much more is known about it.

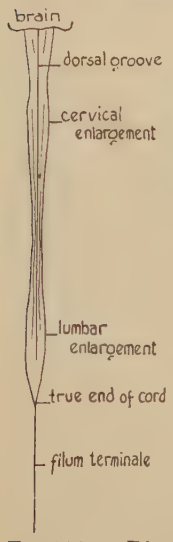


FIG. 550. — Diagram of the human cord, dorsal view, showing enlargements and *filum terminale*.

With its ensheathing envelopes removed, it is seen to be a slightly flattened tube, having a median furrow running down its dorsal length (Fig. 550), and another wider but shallower groove along the middle of the ventral side. These two furrows apparently almost pinch off the cord into two symmetrical halves. Other less conspicuous longitudinal furrows are also present, giving the whole cord somewhat the appearance of a fluted column.

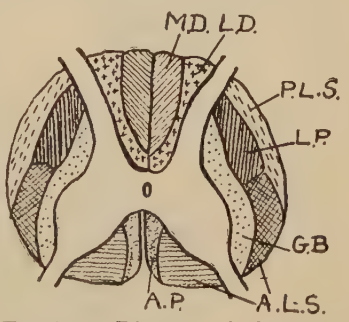


FIG. 551.—Diagram of the nerve tracts in the cord of the neck region of a higher mammal. *M.D.*, median dorsal; *L.D.*, lateral dorsal; *P.L.S.*, posterolateral spino-cerebellar; *L.P.*, lateral pyramidal; *G.B.*, ground bundles; *A.L.S.*, anterolateral spino-cerebellar; *A.P.*, anterior pyramidal. (After Flechsig and Köhler.)

All of these furrows, or *fissures*, are the result of an excessive growth and expansion of the lateral walls of the tube, while the dorsal and ventral regions increase comparatively little in thickness, and so simply constitute the floor at the bottom of the fissures. The tubular character of the cord is considerably camouflaged for the superficial observer, since the central canal is relatively small, extending inconspicuously through the lengthwise bridge that joins the two halves (Fig. 551).

The anterior end, where the cord passes over continuously into the brain, appears broad and somewhat oval in cross section, but at the posterior end it tapers rapidly and finally terminates in a non-nervous threadlike prolongation, called the *filum terminale* (Fig. 550), into which, in early fetal stages, the central canal extends.

At two regions, in the neighborhood of the arms and legs, the cord becomes swollen to an increased size (Fig. 550). That these enlargements are associated with an increased nerve supply of the paired appendages is indicated by the fact that they are absent during embryonic growth before the limbs develop. In flying bats, as would be expected, the anterior far exceeds the posterior enlargement in size, while in the leaping kangaroos, which have more or less rudimentary fore legs, the reverse is true. Certain gigantic dinosaurs of the remote past, that were stilted upon a colossal underpinning of pillar-like legs, for example, *Brontosaurus* (Fig. 33 G), actually had a considerably greater diameter in the sacral region of the cord than in the brain itself, which inspired "B. L. T." in the *Chicago Tribune* to write:

> "You will observe by these remains
> The creature had two sets of brains—
> One in his head (the usual place),
> The other at his spinal base.
> Thus could he reason *a priori*
> As well as *a posteriori*.
> No problem bothered him a bit.
> He made both head and tail of it.
> If something slipt his forward mind
> 'Twas rescued by the one behind.
> And if in error he was caught
> He had a saving afterthought."

2. Extent

In a typical human adult the nervous part of the cord from the point where it leaves the brain at the foramen magnum of the skull to the beginning of the non-nervous filum terminale, reaches only about eighteen inches, or to near the level of the first lumbar vertebra. Thus, the entire axial central nervous system, including brain and cord, extends only from the region of the forehead to the "small of the back."

Embryologically, as well as phylogenetically, the cord originally

is practically as long as the backbone itself. In *Ornithorhynchus* and a few rodents it reaches as far as the sacrum, but there is a pronounced evolutionary tendency for it to shorten.

Among insects this process of cephalization, or shrinkage of the cord, is very striking. The "lower" insects have a primitive nerve chain extending along the entire floor of the body, while "higher" forms present a condensed cord, composed of ganglia that have joined together into compact masses. During the metamorphosis of an insect, such as a honey-bee, for example, a ganglionic chain stretches the whole length of the long larval body, whereas in the adult worker bee that eventually emerges from this larva, the nerve chain is represented by ganglionic masses that are drawn much more closely together (Fig. 552).

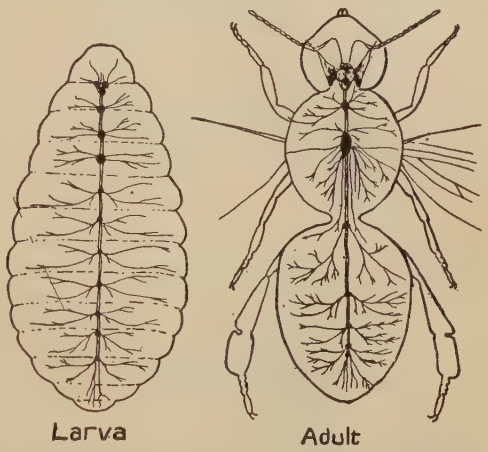


FIG. 552.—Nervous system of a honey-bee, larva and adult, compared to show the concentration of ganglia. (After Blanchard.)

In primates the degree of shortening marks the relative position in animal aristocracy which each occupies, as the following table shows:

Lemur	cord ends at the			7th	lumbar	vertebra
Marmoset (*Hapale*)	"	"	"	6th	"	"
Monkey (*Macacus*)	"	"	"	4th	"	"
Man	"	"	"	1st	"	"

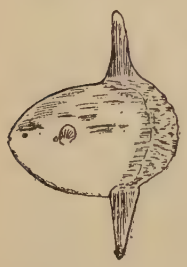


FIG. 553.—A marine sunfish, *Orthagoriscus*, with a cord hardly longer than the brain. (After Meek.)

It is interesting to speculate as to the possible fate of the shrinking nerve cord in the far distant future. Probably the time will never come when the cord will be entirely dispensed with, since there must always remain a structure of sufficient length to furnish a point of departure for the nerves supplying the body. However, certain bizarre fishes (for example *Orthagoriscus*, Fig. 553), quite aside from the main cur-

rent of evolutionary progress, have become so specialized in the form of the body, as to have a cord hardly as long as the brain itself.

3. Internal Architecture

With the formation of the medullary tube there is established around the central canal, above and below, a roof and a floor region respectively which do not increase notably in thickness, and two sides that enlarge enormously until they overshadow both roof and floor, causing the formation of the dorsal and ventral fissures of the cord. Epithelial cells derived from the medullary plate, form the walls of the medullary tube, differentiating

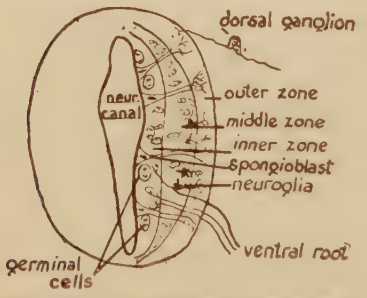


FIG. 554.—Diagrammatic section of the human spinal cord at the sixth week, showing three zones of differentiation. (After Keith.)

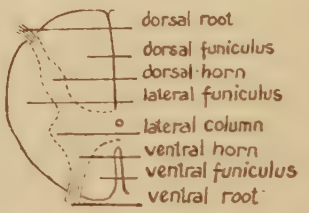


FIG. 555.—Diagram of a cross section through one half of the spinal cord, showing the arrangement of the funiculi of white matter and the columns of gray matter. (After Herrick.)

into the *ependymal* cells, non-nervous *spongioblasts*, and *neuroblasts*, of which the latter eventually become neurones.

The spongioblasts and ependymal cells become stratified into three zones that are particularly apparent in the region of the thick lateral walls. The cells of the inner zone, bordering directly upon the central canal, are columnar ependymal cells, which are ciliated in fetal life and may extend like girders from the central canal to the outer surface of the cord. In the middle and outer zones, the spongioblasts form a skeletal supporting meshwork of spider-like *neuroglia cells* (Fig. 554).

The embryonic neuroblasts collect, for the most part, within the neuroglial meshwork of the middle zone, where they increase rapidly and group together into two main columnar masses, dorsal and ventral, with an intermediate lateral mass in between (Fig. 555). The dorsal, or *alar*, area is given over to fibers of *afferent*,

or *sensory neurones*, bringing in impressions from without, while the ventral, or *basal*, area becomes headquarters for *efferent*, or *motor neurones* that convey messages outward to various effector mechanisms.

Since the neurones of the alar and basal areas intervene between sense organs of the outer surface and the voluntary muscles of the body, they are termed *voluntary somatic neurones*, as contrasted with the *involuntary visceral neurones* which appear in the *intermediate lateral* area. The visceral neurones are similarly made up of sensory and motor units, and provide for the more or less underground activities of the visceral organs.

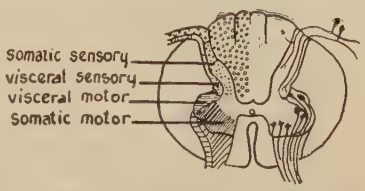


FIG. 556.—Diagrammatic transverse section through the human spinal cord, showing the location of the four types of neurones. (After Herrick.)

Thus, in the middle zone of the lateral wall of the cord there are grouped four kinds of neurones, in order from dorsal to ventral, as follows: somatic sensory; visceral sensory; visceral motor; and somatic motor (Fig. 556). Together they constitute a mass of tissue popularly known as "gray matter," which in cross section somewhat resembles a capital letter H, with a hole (the *central canal*) through the center of the crossbar. The gray matter on one side is continuous with that on the other side by means of the *gray commissure*, a bridge of gray substance enclosing the central canal and for the most part on the dorsal side of it.

The outer zone of the cord is primarily occupied by a nonnervous network of neuroglia cells. Into this network, which serves as a scaffolding, penetrate the lengthening, somewhat parallel fibers of the sprouting neurones, forming *fiber tracts* for transmission and making up the "white matter" of the cord, which surrounds the gray matter on all sides. The reason why the fibrous transmission part of the cord is "white" and the remaining inner part "gray," is because the sheaths on the fibers of the neurones appear white, while the masses of cell bodies without sheaths present a grayish appearance. White fibers with a medullary sheath are present both as dendrites and neurites of sensory neurones, but only as neurites of motor neurones.

The white fibers come from cell bodies located (1) in the cord itself; (2) in the dorsal ganglia outside the cord; and (3) in the brain.

They constitute highways of communication between more or less distant parts.

The general fiber tracts are separated by the horns of the gray matter and the roots of the spinal nerves into three groups, namely, *anterior*, *lateral*, and *ventral funiculi* (Fig. 551).

As would be expected the various paths in the Great White Way of the nerve cord are much more definite in higher forms than in lower vertebrates. According to their general functions they may be grouped in the following manner, as they appear in the cross section of the human cord:

I. *Ascending sensory tracts*
   1. Dorsal columns
      Median (*fasciculus gracilis Golli*)
      Lateral (*fasciculus cuneatus Burdachi*)
   2. Spinal cerebellar system
      Posterolateral (*fasciculus cerebello-spinalis*)
      Anterolateral (*fasciculus antero-lateralis superficialis Gowersi*)
   3. Spino-bulbar system

II. *Descending motor tracts*
   1. Cortico-spinal system
      Lateral crossed pyramidal tract (*fasciculus cerebro-spinalis lateralis*)
      Anterior direct pyramidal tract (*fasciculus cerebro-spinalis anterior*)
   2. Bulbo-spinal system

III. *Association ground bundles*
   1. Lateral (*fasciculus lateralis proprius Flechsigi*)
   2. Anterior (*fasciculus anterior proprius Flechsigi*)

A. Ascending Sensory Tracts

The fibers which give rise to the dorsal columns, are neurites coming from neurones located in the dorsal ganglia outside the cord. As they come in, forming the dorsal root of the spinal nerve, they branch and go both ways, toward and away from the head, thus making the dorsal columns. Both the ascending craniad fibers, and the shorter descending caudad fibers, send off collaterals that enter the basal area of the gray territory, where they form synapses with somatic motor neurones located there. Many of the cranially directed fibers may reach as far as the brain itself.

The afferent dendritic processes of these same neurones extend outward from the dorsal ganglia where the cell bodies are located, to connect with receptors, or to serve themselves as receptors. Thus, a line of communication is made complete between the

stimuli of the outside world and the effectors of the body, by way of the adjusting center of gray matter in the cord or in the brain.

The dorsal columns are composed principally of two tracts, wedge-shaped in cross section, the inner median one next to the dorsal fissure being the *Column of Goll*, and the lateral one next to the gray matter, the *Column of Burdach*, so named in honor of two neurological pioneers (Fig. 551, M.D. and L.D.).

In fishes the dorsal columns are poorly developed, because outside stimuli are largely received through the lateral line sense organs which are supplied by a branch of the Xth cranial nerve (*vagus*), and so carried directly to the brain, instead of indirectly by way of the nerve cord.

In the lateral funiculus, included between the dorsal and ventral roots of the spinal nerves, the two most conspicuous tracts of white fibers constitute the *lateral spino-cerebellar system.* They are by no means as well defined, or so peripheral in position, among fishes and amphibians as in the higher vertebrates. One of these tracts, the *posterolateral spino-cerebellar tract* of Flechsig, is made up of fibers that reach the brain, with their cell bodies in the dorsomedian region (*Clark's Column*) of the gray area on either side of the central canal. The other, or *anterolateral spino-cerebellar tract*, is an ascending bundle of fibers, the cell bodies of which likewise lie in the dorsal region of the gray area, while their neurites lead directly, or by relay neurones, to the cerebellum of the brain.

Associated intimately with the spino-cerebellar highways are various other lesser tracts that reach different regions of the brain, and form the *spino-bulbar system*, which carries impulses of the cutaneous senses of pain, temperature, and touch. The neurones of these tracts are located in the gray matter on the side opposite from that occupied by the fiber tract itself, and so a crossing over, by way of the gray commissural bridge around the central canal, is made necessary.

B. Descending Motor Tracts

The *cortico-spinal system*, on the other hand, runs from the brain to the cord, constituting a motor transmission highway peculiar to mammals. It arises from cell bodies in the cortex of the cerebrum, in the anterior part of the brain, and grows down by means of its neurites into the cord, eventually reaching the

ventral horn of the gray area to synapse with the neurones there, whose fibers extend outward through the ventral roots of the spinal nerves to the effector mechanisms.

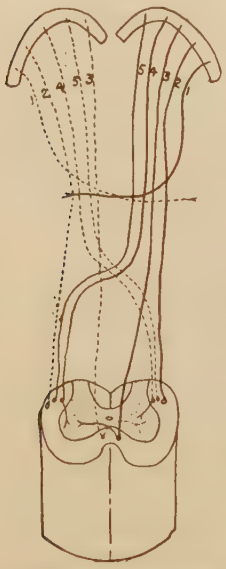


FIG. 557. — Diagram representing the course of the fibers of the pyramidal system. *1*, fibers to the nuclei of the cranial nerve; *2*, uncrossed fibers to the lateral pyramidal fasciculus; *3*, fibers of the anterior pyramidal fasciculus, crossing in the cord; *4* and *5*, fibers that cross in the pyramidal decussation to make the lateral pyramidal tract of the opposite side. (After Howell.)

The cortico-spinal fibers do not all follow the same course. Most of them, upon reaching the posterior part of the brain (*medulla*), cross over from the side of their cortical origin and enter the cord on the opposite side, forming the *lateral crossed pyramidal tracts*, which are surrounded by the spino-cerebellar bundles in the lateral funiculus of the cord (Fig. 557). These tracts together form "a great motor strand which brings the spinal motor apparatus under the control of the will" (Cunningham). Other fibers, fewer in number, continue from cortex to cord on the same side of their origin, forming the anterior *direct pyramidal tracts*, that come to lie on either side in the anterior funiculus close to the ventral fissure on the medial side.

These latter tracts are found only in the anthropoid apes and in man. Just before the fibers composing them terminate, they also cross over within the cord and synapse with motor neurones of the side opposite from their origin, so that finally all the neurones of the cortico-spinal system make connections with effector neurones on the side of the body opposite to the cell bodies in the brain from which they originate.

Other lesser descending bundles, which may be grouped together as the *bulbo-spinal system*, return from different parts of the brain to the cord and aid in the complicated regulation of the effectors of the body.

C. Association Ground Bundles

Immediately around the gray area of the cord are the *association ground bundles*, composed of short fibers of neurones,

whose cell bodies are in the gray region, and consequently remain entirely within the cord, connecting different systems.

The *lateral ground bundle* is in the lateral funiculus, while the *anterior ground bundle* makes up the bulk of the anterior funiculus between the direct pyramidal tract, when present, and the ventral root of the spinal nerve.

Some of the association neurones of the ground bundles also cross over to the opposite side, thus weaving together and unifying the whole transmission apparatus.

4. Comparative Anatomy of the Cord

In amphioxus there is no gray and white differentiation. The medullary groove is still open (Fig. 558), and thus the central canal lies at the bottom of what appears at first to be the dorsal fissure. There is no dorsal fissure, however, for there is no excessive thickening of the lateral walls, which is the necessary accompaniment of the formation of a fissure. Only a few scattering neurones are present, collected mostly along the approximated edges of the medullary groove and extending their fibers out through the network of neuroglia cells that make up the bulk of the cord, where they appear in cross section as isolated groups of a few scattered fibers each.

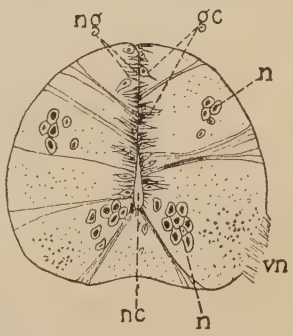


Fig. 558. — Cross section through the nerve cord of amphioxus, showing *n*, large nerve fibers; *vn*, ventral nerve; *nc*, neural canal; *ng*, neuroglial cells, and *gc*, ganglion cells. (After Haller.)

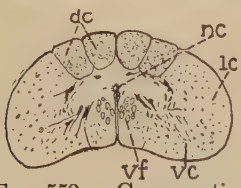


Fig. 559. — Cross section through the nerve cord of the lamprey eel, *Petromyzon*. *dc*, dorsal columns; *lc*, lateral column; *nc*, neural or central canal; *vc*, ventral columns; *vf*, ventral fibers. (After Haller.)

In general the cross section of the cord is somewhat triangular, rather than circular or oval.

In the lamprey eel, *Petromyzon* (Fig. 559), the cord has become truly tubular, and, although the gray and white areas are still undifferentiated except in the dorsal columns, and still appear to be rather indefinitely established, the increase in the thickness of the sides has begun, preliminary to tissue formation, as seen in the widened cross section.

Bony fishes present a dorsal but no ventral fissure, and the general shape in cross section is round rather than flattened (Fig. 560). The dorsal columns are quite evident and the gray matter begins to be somewhat in evidence around the central canal.

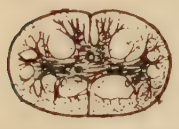


Fig. 560. — Cross section through the nerve cord of a teleost fish, *Salmo*. (After Bütschli.)

A shallow dorsal, as well as ventral fissure, is established in amphibians, and from this group on, the fiber tracts become more and more distinct.

In mammals the lateral crossed pyramidal tracts are added, and finally in anthropoid apes and man the anterior direct pyramidal tracts.

The pattern of the gray and white matter, as well as the actual size of the cord, varies greatly at the different levels of any in-

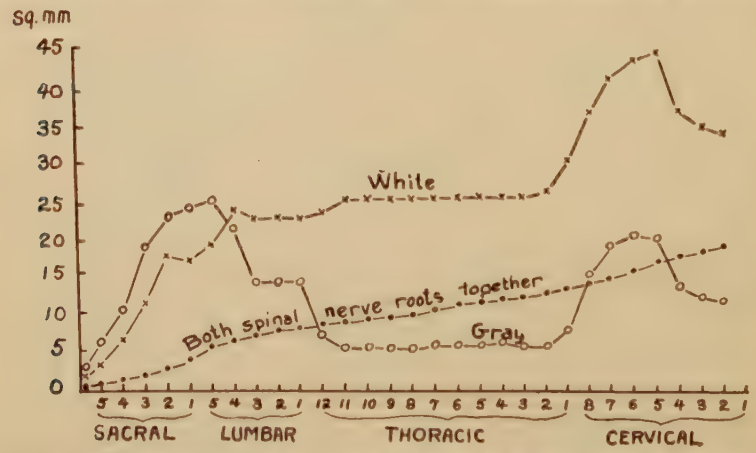


Fig. 561.—Diagram showing by curves the area, at several levels of the cord, of the white and gray matter, and of the roots of the spinal cord. (After Donaldson, compiled from measurements by Stilling.)

dividual. Since the white is the transmission highway between the cord and the brain, it naturally becomes cumulatively larger the nearer it comes to the brain itself. The relative amount in square millimeters of the white and the gray throughout the human cord, is shown by the curves plotted in Fig. 561.

VII. MENINGES

The precious central nervous system is surrounded with wrappers of various sorts. The inner envelopes, immediately around

the cord itself, are termed the *meninges*. In the higher vertebrates there are three meninges, which from the inside out are the pia mater, the arachnoidea, and the dura mater.

The *pia mater* bears blood vessels and consequently has a nutritive mission. It fits with tailor-like snugness close around the cord, descending into the fissures and every unevenness of the surface. Outside the pia is the *arachnoid* layer, forming a spiderweb meshwork of great delicacy, hence its name. This is succeeded by a tough connective tissue of protective nature,

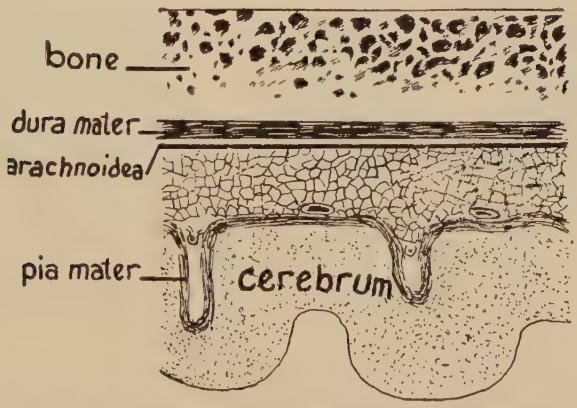


FIG. 562.—Scheme of the general relations of the meninges to the brain. (After Rouvière.)

the *dura mater*, which fits within the skeletal envelope, that is, the neural arch of the vertebræ.

In the cranium the dura mater serves as the inner periosteum of the skull bones (Fig. 562), but in the cord it is not in direct contact with the bony neural arch of the vertebræ, being separated from it by an *epidural space* filled with fluid. In addition the space between the dura mater and the arachnoidea (*subdural space*), as well as that between the arachnoidea and the pia mater (*subarachnoid space*), which is relatively of considerable size, is filled with a lymphlike cerebro-spinal fluid, forming jackets of lubricating material that serve as shock absorbers, making possible the movement of the vertebræ upon each other without causing mechanical injury to the cord.

The skeletal encasement is in turn overlaid by a thick pad of muscles and tendons, and finally, by the skin. Frequently the

skin itself is rendered more protective on the outside by scales, bony dermal plates, feathers, or fur.

In fishes there is but a single meningeal layer, the *meninx primitiva*, but close to the cord and lining the skeletal archway through which the cord extends, there is also in all vertebrates an endosteal tissue, the *endorachis* (Fig. 563, A).

In amphibians, reptiles, and birds, the meninx primitiva becomes split into dural and pial layers, with a subdural space

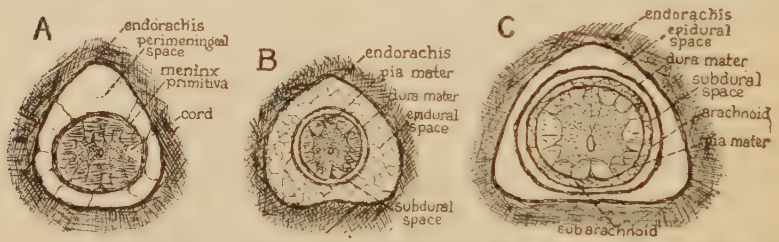


FIG. 563.—Diagrams of the meninges in the chief groups of vertebrates. *A*, fishes; *B*, amphibians and sauropsidans; *C*, mammals. (From Wiedersheim, after Sterzi.)

between, while in mammals the inner pial layer is further differentiated into the arachnoid and the pia mater.

The complete list of the envelopes of the mammalian cord, is as follows: pia mater, subarachnoid fluid, arachnoid, subdural fluid, dura mater, epidural fluid, endorachis, vertebral arch, muscles, and skin. Within the cranium the endorachis and dura mater are continuous, not being separated by a fluid-filled epidural space.

VIII. BRAIN

1. In General

Professor Keith characterizes the human brain as "Nature's master contrivance," yet it must be remembered that the great majority of organisms on the earth fill out their cycle of existence, accomplishing successfully the two major activities of self-maintenance and the continuation of their kind, without the aid of so elaborate a mechanism. Nevertheless, with a human brain it becomes possible *to live a human life*, which involves something more than metabolism and reproduction. This lofty goal has been gained, however, as comparative biology reveals, only after much evolutionary travail.

The vertebrate brain is the enlarged end of the nerve cord. Like the cord it is a continuous tubular structure, the walls of which are composed of neurones that are arranged in communicating tracts and adjusting centers, and are supported and protected by non-nervous elements.

The brain becomes differentiated from the cord as the result of a mobilization of nerve elements in the neighborhood of the important sense organs of smell, sight, hearing, and taste, which are on guard near the entrance to the digestive canal. Whenever these sense organs are reduced or absent, as in deep-sea or cave animals, or in sessile forms, the brain diminishes to a corresponding degree.

Although the sense organs of the head unquestionably take a prominent part in determining the modifications of the brain, yet they by no means set the limit to its differentiation, as there

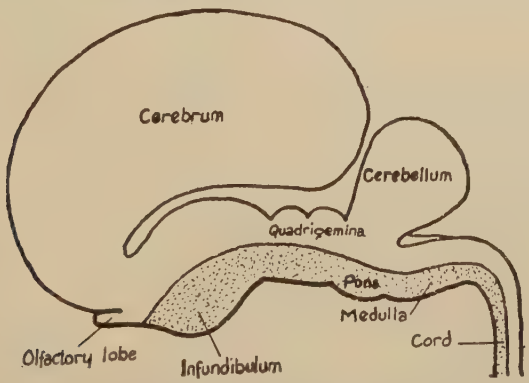


FIG. 564.—Dorsal sensory and ventral motor regions of the brain. (After Minot.)

are many animals with inferior brains, whose sense organs are superior to those of man. It is the establishment of *associative centers* that forms the outstanding feature of the brain, for its general mass and contour, unlike that of the cord with the brachial and lumbar enlargements of the latter, are not solely dependent upon the area of stimulus-receiving surface involved or the amount of musculature and glandular tissue supplied.

In other words, the conspicuous enlargements which characterize the walls of the brain, are not so much due to incoming and outgoing limbs of reflex arcs that relate the animal di-

rectly to its environment, as to internal associative connections which, at least in man, enable the brain that "sits in darkness" not only to reconstruct the outside world but also to preserve the accumulations of memory and even to provide for creative flights of imagination.

Fig. 565.—Central nervous system of amphioxus, showing alternating spinal nerves and photoreceptor cells, represented by dots, embedded in the nerve cord. (After Owajannikow.)

The primary axis, or stem, of the brain is directly concerned with peripheral nerve relations, the motor centers and pathways, both somatic and visceral, being located along the ventral region, as in the cord, while the sensory somatic and visceral neurones occupy the larger dorsal area (Fig. 564). Upon this primary cord-like axis of simple reflex-arc systems, is superimposed the relaying association centers of correlation and coördination, as best exemplified by the complex cerebrum and cerebellum, which are once removed from direct sensory reception and muscular response. *Correlation centers* concern the adjustment of incoming sensory stimuli, while *coördination centers* regulate the outgoing motor responses. These superimposed centers of the brain may be compared to the switchboard of a telephone exchange, where messages are received and redistributed.

Fig. 566.—The relatively small brain of *Brontosaurus*. (After Marsh.)

2. Comparison of Brain and Cord

The central nervous system of amphioxus is all cord and no brain (Fig. 565). The true rise of the brain begins in fishes, where the cord still remains heavier than the brain. Among amphibians the brain overtakes the cord in bulk and weight, while in modern reptiles the brain comes to take the lead, which, ever afterwards in the vertebrate series, is maintained. The relatively small brain of primitive reptiles is indicated in Fig. 566.

In mammals there is an ascending dominance of the brain over the cord. A cat and a macacque monkey, for example, with cord of the same weight (7.5 grams), have been found with a brain weighing 29 and 62 grams respectively, or ratios

of approximately 1:4 and 1:8. The relation in man is nearer 1:50, an average sample measurement being 26 grams for the cord as compared with 1350 grams for the brain.

3. Differentiation of the Brain

The transformation of the simple tubular brain into the exceedingly complex structure found in man, is brought about through the following phases of growth: (A) constriction; (B) unequal thickening of the walls; (C) invagination and evagination; and (D) bending.

A. Constriction

The original, somewhat enlarged, anterior region of the cord, formed by the closure of the medullary groove, is called the *encephalon.*

Very early in embryonic life, the third week in man, the encephalon becomes marked off into three regions by two constrictions (Fig. 567, B). These primitive regions are designated as the *prosencephalon, mesencephalon,* and *rhombencephalon,* the latter so called because of the kite-shaped appearance of the ventricle showing here, due to the widening of the medullary tube in this region.

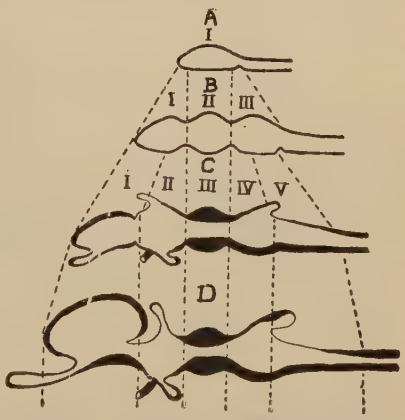


Fig. 567.—Diagrams of the encephalon and its evolution. *A*, primitive encephalon; *B*, division into prosencephalon, mesencephalon, and rhombencephalon; *C* and *D*, further division into the five regions of the brain. (After Roule.)

A little later, the fourth week in man, the prosencephalon becomes further constricted into two subregions, the *telencephalon* and the *diencephalon.* The rhombencephalon likewise, about the fifth week in man, is subdivided into a *metencephalon* and a *myelencephalon,* the mesencephalon remaining unconstricted. The brain is now marked off into five definite areas (Fig. 567, C), arranged in order from anterior to posterior as follows: telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon.

Certain of these primary regions of the brain are destined to

take on a special importance, because of the sense organs with which they are intimately connected. The telencephalon may be regarded as the "nose brain," the mesencephalon, the "eye brain," and the myelencephalon, the "ear brain," as well as the "skin brain" and the "visceral brain."

Cyclostomes throughout life remain with the brain constricted into only three regions, but from fishes on, the five fundamental parts of the brain are clearly represented.

B. Unequal Thickenings of the Walls of the Brain

The walls of the primitive encephalon are at first of approximately equal thickness, but as neurones develop and collect into centers and transmission tracts, the disposition of these collections of nerve elements brings about decided contrasts in the thickness of the brain walls in different places (Fig. 568).

Beginning at the posterior end, the variation is quite pronounced in the *myelencephalon*. The dorsal wall, *velum*, retains its em-

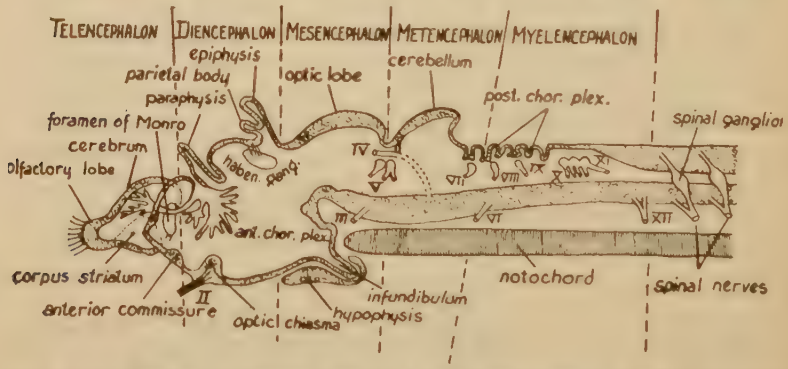


Fig. 568.—Sagittal diagrams through a vertebrate brain, showing the five general regions and the variations in thickness of the brain wall. (After Bütschli.)

bryonic thinness, while the sides and ventral regions, constituting the *medulla*, become quite thick, on account of forming the main highway of fiber tracts between the cord and the brain, and also, of being the center of origin for most of the cranial nerves, as well as headquarters for numerous reflexes.

In the *metencephalon* the continuous thin dorsal wall of the myelencephalon suddenly becomes excessively thickened to form the *cerebellum* in the higher vertebrates, which is perched upon the main axis of the brain stem. The lateral parts of the

metencephalon are largely the paired *peduncles*, posterior, median, and anterior, which are like three pairs of legs for the cerebellum to stand upon, and are mostly composed of fiber tracts. The median peduncles are continuous with each other around the ventral side of the metencephalon, forming the *pons*, which resembles the band of a seal ring, with the cerebellum representing the seal.

The *mesencephalon* thickens in a lesser degree, both dorsally and ventrally, yet presents notable enlargements, particularly in the lower vertebrates. The dorsal part is thrown up into two elevations, the *optic lobes*, while the ventral region of the fiber tracts forms the *crura cerebri*, which are important carriers between the cord and the anterior centers of the brain. A constriction which originates as far down as reptiles and birds, definitely divides the optic lobes in mammals into two pairs of small dorsal elevations, the *corpora quadrigemina*, the posterior pair becoming centers of hearing, while the centers of sight are now confined to the anterior pair.

The roof of the *diencephalon*, which remains thin and nonnervous, is the locus for various problematical structures to be referred to in the next section.

The thick sides of the diencephalon, known as the *thalami*, continue forward to form an exclusive bridge of fiber tracts from the posterior part of the brain and from the cord to the anterior centers, and also to provide room for certain relay centers, while the floor of the diencephalon, that like the roof is also thin and unprovided with centers and tracts, is pushed down to form a pocket-like depression, the *infundibulum*.

The *telencephalon* extends out from the anterolateral region of the diencephalon as a paired structure, the *cerebrum*, the walls of which take on enormous enlargement and thickening, so that eventually in mammals the cerebral lobes entirely overshadow and cover up both the diencephalon and the mesencephalon, concealing them from dorsal view. The ventral fiber tracts of the telencephalon, the *corpora striata*, are also massive, forming a thick brain wall.

C. Invaginations and Evaginations

There are two places where the brain wall is pushed in or invaginated, namely, in the region of the thin roofs of the myelen-

cephalon and the diencephalon. Over the outside of these thinnest places in the walls of the brain, extends a network of capillaries in the pia mater that intimately envelops the brain. These capillary nets are the *chorioid plexuses*, which by invagination are pushed down into the cavities below, carrying the thin wall ahead of them. They provide a blood supply for the inside of the brain.

In the thin walls of the diencephalon there also occur various evaginations. On the dorsal side in certain vertebrates, behind the invaginated anterior chorioid plexus, are two finger-like outpushings of the wall, one behind the other. The anterior evagination, near the junction of the cerebral lobes and the diencephalon, is the *parietal organ*, which is particularly developed in certain reptiles, while the posterior projection, the *epiphysis*, or pineal gland, appears in some stage of elaboration or degeneration in practically all vertebrates.

A ventral median evagination of the floor of the diencephalon, the *infundibulum*, has already been mentioned. It joins a glandular upgrowth from the roof of the mouth to form the hypophysis which, like the pineal body, has been briefly considered in Chapter XVI as a gland of internal secretion.

In early embryonic life there extend outward from the sides of the diencephalon, two evaginations of the walls that later become the *optic stalks*, giving rise at their ends to the *optic cups*, from which the retinas of the eyes develop.

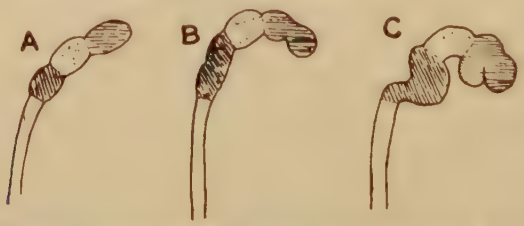


Fig. 569.—Stages in the process of making the brain more compact. (After Rouvière.)

D. Bending

In cyclostomes and other lower vertebrates, the brain retains its primitive straight form, but with the onrush of growth and the ultimate confining limits of the skull, it becomes necessary for the brain stem to bend and fold into more compact quarters (Fig. 569). The bends, or flexures, of the brain are typically three: (1) the

parietal flexure in the region of the mesencephalon; (2) the *cervical flexure* near the junction of the cord and the medulla, both of which bend dorsally or outward, and (3) the *pontine flexure* between these two in the region of the metencephalon bending in the opposite direction, thus tending to kink the brain like a compressed accordion (Fig. 570).

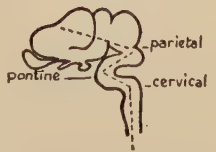


Fig. 570. — Diagram showing the flexures of the brain.

4. Ventricles

As a result of the process of invagination, the central nervous system of vertebrates is hollow. In the cord the cavity forms a *central canal*, which remains very small and approximately uniform in size throughout its length. Continuous with the central canal, and like it filled with cerebro-spinal fluid, are the cavities, or *ventricles*, of the brain (Fig. 571). These are chambers of unequal dimensions and frequently encroached upon but never entirely obliterated by the thickening walls of the brain itself.

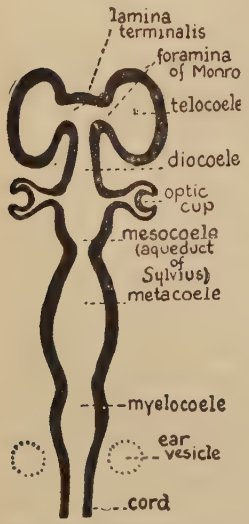


Fig. 571.—Frontal diagram to show the cavities of the brain.

The most posterior chamber, the myelocœle located in the myelencephalon, is enlarged into a widened space covered over by the thin velum. In ordinary dissection the velum is frequently torn away, exposing the myelocœle as a triangular trough on the dorsal side of the medulla.

The *metacœle*, or cavity of the metencephalon, is very much compressed and nearly obliterated by the upward thrust of the cerebellum from the primary axis of the brain, nevertheless it represents a continuous passage-way from the myelocœle behind to the *mesocœle*, inside the mesencephalon, in front. Together the myelocœle and the metocœle are sometimes designated as the *fourth ventricle* and the mesocœle as the *aqueduct of Sylvius*, which in turn leads into the *diocœle* or *third ventricle*, within the diencephalon. The true anterior end of the cavities of the brain is set by the *lamina terminalis*, or anterior wall of the diencephalon. The paired telencephalon extends forward laterally from this region to

form the two large cerebral lobes which are hollow. The cavities within the cerebral lobes are called *telocœles*, or the *first* and *second ventricles*, and communicate with the diocœles on either side through a narrow passage-way, named the *foramen of Monro* in honor of three generations of Scotch surgeons, father, son, and grandson, who together made the notable record of holding with distinction the chair of Anatomy in the famous University of Edinburgh for one hundred and twenty-six consecutive years, from 1720 to 1846.

The anterior chorioid plexus invaginates into the diocœle. Other similiar plexuses may extend through the foramina of Monro on either side into the telocœles, where they bring a blood supply to the inner recesses of the cerebrum.

It is now desirable to consider a little more closely each of the five regions of the brain in order to determine something of the contributions which each makes to the structure as a whole.

5. Regions of the Brain

A. Myelencephalon

The dividing point between the brain and the cord is an arbitrary one, determined by the relation to the foramen magnum of the cranium. It is to be expected that the myelencephalon would present many points of likeness to the cord, and the German name of "das verlängerte Mark" (elongated cord), is an excellent descriptive term for the medulla, which makes up the bulk of the myelencephalon.

The cerebellum of the brain, conspicuous in most vertebrates, may be wanting, for instance, in cyclostomes and some amphibians, and the dominant cerebrum may be dispensed with in teleost fishes, but no vertebrate is without a medulla.

The sides of the medulla, like those of the cord, are composed of a dorsal *alar area* and a ventral *basal region*, separated by a borderline groove, the *sulcus limitans*. As in the cord, these areas are further differentiated primarily into the ependymal lining around the myocœle, an inner zone of neurones, and an outer fiber-tract region. Both the floor and the roof of the myelencephalon, however, become considerably modified from the indifferent condition typical for the cord.

Because of the formation of the pontine flexure and the lateral bulging of the alar plates, the roof becomes stretched out, particularly in the anterior region, into the broad, thin, non-nervous

velum interpositum, while the originally non-nervous floor plate is so encroached upon from either side by the fiber tracts of the basal plates of the lateral areas, that the thick lateral walls become continuous ventrally with each other (Fig. 572).

Further differentiation of the myelencephalon is marked by the presence of centers for several of the cranial nerves, by the passing through of fiber tracts, and by the establishment of relay centers, or *nuclei*.[1] The various nuclei of the medulla control the reflex

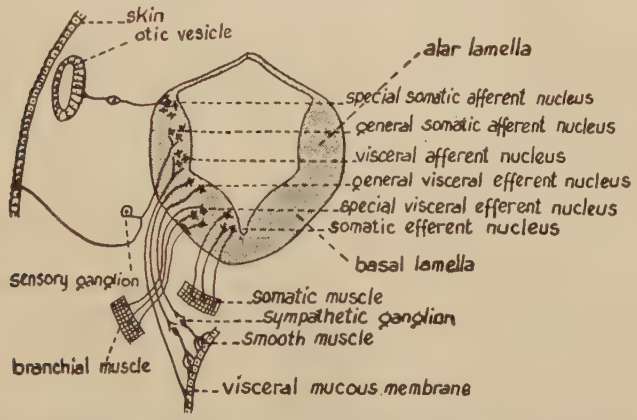


FIG. 572.—Diagrams of the different types of neurones that form the columns of gray matter in the medulla. (After Ranson.)

activities of the tongue, pharynx, larynx, and, in part, of the lungs and the viscera in the body cavity.

The definite arrangement of the gray and white matter characteristic of the cord, is broken up in the medulla by the presence of numerous nuclei in the myelencephalon and by fiber tracts which tend to decussate, that is, to cross over to the opposite side, as well as by the relaying of the fibers from the dorsal columns of the cord.

On the ventral aspect of the medulla are to be seen two longitudinal swellings, the *pyramids*, lying side by side, and separated from each other by a continuation of the ventral fissure of the cord. They are composed largely of the pyramidal fiber tracts

[1] The term "nucleus," as used by neurologists, to designate a group of cell bodies clustered together inside the central nervous system, in contrast with a *ganglion*, when a similar group of neurones are found together outside of the central nervous system, is rather unfortunate, since it is a word which cytologists use technically to express a different idea.

that extend from the gray cortex of the brain back to the cord. In the posterior region of the pyramids, the larger part of these fibers cross over to the opposite side to become the crossed pyramidal, or cortico-spinal tracts, (Fig. 557), the region of crossing, which interrupts the ventral fissure, being the *decussation of the pyramids.* The reason for decussation is not known. Uncrossed fibers remain on the side of their origin and become the ventral pyramidal cortico-spinal tract of the cord.

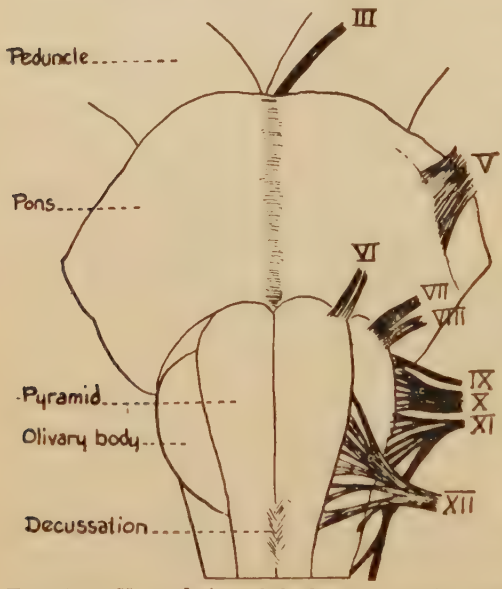


FIG. 573.—Ventral view of the brain stem, showing the exit of the cranial nerves. (After Bing.)

The lateral areas of the medulla, that lie between the dorsal and ventral roots of the cranial nerves, are continuations of corresponding areas of the cord, which contain the cerebellar tracts, both lateral and anterior. In mammals anteriorly, on either side in the lateral region of the medulla are the *olivary bodies* of unknown function, that appear as oval swellings (Fig. 573). These bodies are centers, or "nuclei," with fibers leading to the cerebellum from the cord, and from the thalamus in the diencephalon.

The dorsal columns of the medulla, which spread out or rotate laterally in position, contain two pairs of prominent nuclei, the *nucleus gracilis* and *nucleus cuneatus.* These relay the sensations transmitted through the columns of Goll and of Burdach respectively, to the anterior part of the brain by way of the fiber tracts of the *medial lemniscus,* or *fillet.* The fibers of the medial lemniscus, which terminate in the thalamus, also cross over in the medulla, anterior to the motor decussation, and form a second decussation, the *sensory decussation of the lemniscus.* Other nuclei too are present in the medulla.

The *velum*, composed primarily of the layer of ependymal cells that surround the cavity of the brain, serves as a secretory apparatus for the production of cerebro-spinal fluid, and bears the *posterior chorioid plexus* in its anterior part. The non-vascular part of the velum, posterior to the plexus, which covers over the triangular myelocœle, is termed the *metatela*.

B. Metencephalon

The stem of the brain is continued forward from the medulla through the metencephalon, with the added outstanding features in this region of cerebellum and pons.

The *pons*, particularly in mammals, is largely a transverse commissure of the cerebellum, made up of fibers that pass both ways around and across the ventral surface of the stem of the brain in the pyramidal region to reach the opposite side (Fig. 574).

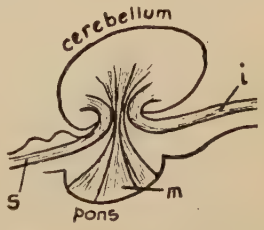


Fig. 574.—Schematic representation of the metencephalon. *s*, superior peduncle; *m*, middle peduncle; *i*, inferior peduncle. (After Piersol.)

The *cerebellum* is a large center concerned with unconscious motor coördination. It is small in creeping, short-legged, or mud-dwelling vertebrates, but large in strong swimmers, runners, and fliers. It arises from the alar part of the brain stem as a transverse dorsal lip at the anterior margin of the myelocœle, and, in cyclostomes and amphibians, remains at the dorsal-lip stage of development throughout life. To the primitive, single, median, cerebellum, or "vermis," of lower vertebrates, however, there are eventually added lateral elements of considerable size, the *hemispheres* and *flocculi* which notably increase the correlation tissue and the conduction tracts composing this organ (Fig. 575).

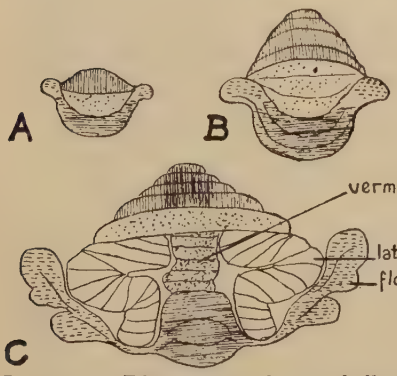


Fig. 575.—Diagram of the cerebellum. *A*, crocodile; *B*, bird; *C*, mammal. Anterior lobe, vertical lines; median lobe, dots; posterior lobe horizontal lines. (From Ranson, after Inguar.)

Beginning with reptiles, both the median *vermis* and the enlarged lateral hemispheres are furthermore divided transversely into three *lobes*, *anterior*, *middle*, and *posterior*, a modification which increases the external surface of the organ still more without appreciable enlargement of its total size. In birds, lateral auricular extensions of the posterior lobe become established, homologous with the flocculi of the mammalian cerebellum.

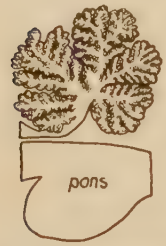


FIG. 576.—Sagittal diagram through the cerebellum and pons, showing the white matter arranged as the "arbor vitæ." (After Ranson.)

Upon sectioning, the cerebellum shows a conspicuous arborescent arrangement of white fibers, the *arbor vitæ* of the older anatomists, surrounded by gray matter (Fig. 576). The latter is stratified into two layers, distinguishable by means of the different character of their component cells. Between the outer, or *molecular* layer, and the inner, or *granular* layer, both of which are composed of neurones, are marshalled in definite array the *Purkinje cells*, with their remarkably elaborate dendrites (Fig. 577). These cells are not only peculiar to the cerebellum, but also of particular interest on account of the supposed part which they play, through the coördination of muscles, in maintaining the equilibrium of the body.

Within the cerebellum, as well as over its outer surface, are various areas of gray matter, or nuclei, the largest being the *dentate nuclei*, which are located inside the core of the cerebellar hemispheres.

FIG. 577. — Purkinje cell of adult human cerebellum. (Golgi preparation.) (After Ramon y Cajal.)

The fibers composing the arbor vitæ enter and leave the cerebellum for the most part by way of three pairs of legs, or *peduncles*, which support the structure upon the brain stem (Fig. 574). The posterior, or *inferior peduncles*, also known as the *restiform bodies*, carry fibers that connect the medulla and the cord with the cortex of the cerebellum. The *median peduncles*, already described as making a transverse commissure for the cerebellum, wrap around

the ventral side of the brain stem, thus forming the bulk of the pons. They are the largest of the three pairs of peduncles in man. The *anterior*, or *superior peduncles* contain fibers that emerge from, or enter into, the dentate nuclei of the cerebellum, and connect, after decussation, with the *red nucleus*, so called because of its vascularity, of the opposite side in the mesencephalon.

C. Mesencephalon

The mesencephalon is conservative, as it undergoes the least phylogenetic modification of any part of the brain. It possibly represents a former pioneer anatomical outpost since once the termination of the primitive neural tube was at the level of the parietal flexure, with the notochord ending directly beneath it. In lower vertebrates, particularly teleost fishes (Fig. 578), where the anterior part of the brain is of relatively insignificant proportions, it becomes the main headquarters of the nervous function.

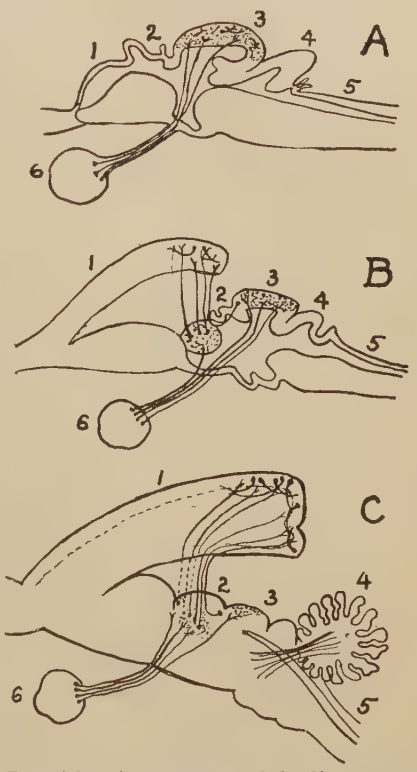


Fig. 578.—Arrangement of the fiber tracts from the midbrain to the cerebrum. The neurones are overemphasized. *A*, fish; *B*, reptile; *C*, mammal. *1*, telencephalon; *2*, diencephalon; *3*, mesencephalon; *4*, metencephalon; *5*, myelencephalon; *6*, eyeball. (After Monakow.)

Notwithstanding an apparent lack of elaboration, its essential importance throughout the vertebrate series is maintained, for it always remains the inevitable highway of the fiber tracts, *crura cerebra*, which connect the cord with the cerebral region.

Not only is the mesencephalon a highway of the fiber tracts, but it is also the location of the nuclei of origin for the third and fourth cranial nerves that activate the muscles of the eye-

ball, as well as for certain other nuclei, such, for example, as the red nuclei, in which fibers are relayed to and from the cerebellum.

On the dorsal side of the mesencephalon the prominent pair of *optic lobes* are centers of sight, as well as of other reflexes in lower vertebrates. In mammals where the subdivision of the optic lobes into the *corpora quadrigemina* occurs, the *posterior*, or *inferior* pair of dorsal elevations that make up the corpora quadrigemina, become concerned with hearing, while the sight centers are confined to the larger *anterior*, or *superior* pair (Fig. 578, C).

D. Diencephalon

The *diencephalon* has many phylogenetic modifications in the different vertebrate classes. It is placed somewhat diagonally between the telencephalon, which is anterior and superior to it on the one hand, and the corpora quadrigemina and crura cerebri of the mesencephalon, which limit it posteriorly and inferiorly.

A section through the region of the diocœle, or third ventricle of an early human embryo (Fig. 579), furnishes landmarks for the various structures found in the diencephalon. The thin nonnervous roof and floor are connected laterally by thicker alar and basal areas of the sides, which are marked off from each other by the *sulcus limitans*. This fundamental relationship of parts may be traced backward through the entire brain stem to the cord.

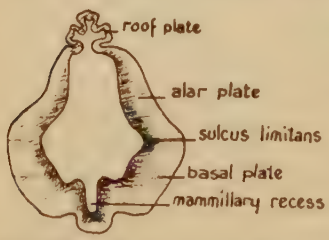


Fig. 579.—Cross section through the diencephalon of a human embryo, 14 mm. in length. (From Arey, after His.)

In the diencephalon the thin roof plate, or *velum interpositum*, becomes overspread by a capillary network which forms the *anterior chorioid plexus*, that pushes down into the diocœle to nourish the inside of the anterior region of the brain.

At the edge of the roof where it joins the lateral alar plate, there forms the *epithalamus*, a thickened ridge giving rise to the rudimentary or degenerate *pineal body*, already considered in Chapter XVI, and the *habenula*, an olfactory center present in all vertebrates.

The alar plates become the *thalami*, large lateral oblong masses wedged between the corpora striata of the telencephalon, and resting posteriorly upon the crura cerebri of the mesencephalon. They are largely composed of gray matter, and contain several nuclear masses of which the most prominent are the *anterior*, *medial*, and *lateral nuclei*. The anterior and medial nuclei are important centers in lower vertebrates in which the telencephalon is poorly developed. The lateral nuclei are large and of more recent phylogenetic origin than the other nuclei of the thalami.

Associated with the lateral nuclei in the posterior region of the thalamus are the *pulvinar* and the *lateral geniculate bodies*, or the

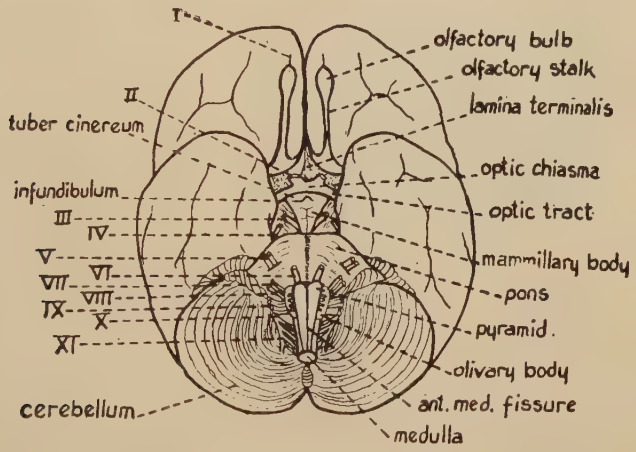


FIG. 580.—Basal aspect of human brain. (After Piersol.)

metathalamus, centers which have to do with relaying visual impressions to the cerebral cortex.

Optical stimuli, however, and also all other nervous impulses that reach the cortical centers of the cerebrum, with the exception of olfactory sensations, must pass through the thalami.

The basal plate of the diencephalon becomes the *hypothalamus*, from which develops the *posterior lobe of the hypophysis*, and two olfactory centers, the median *tuber cinereum*, and the lateral mammillary bodies which lie on either side behind the *tuber cinereum* (Fig. 580). The infundibulum extends down toward the hypophysis, from the tuber cinereum, immediately behind the *optic chiasma*.

Between the mammillary bodies there is also a vascular structure,

the *saccus vasculosus*, which pushes into the infundibulum, carrying the epithelial layer of the brain wall with it. This vascular mass is large in fishes but degenerate in mammals.

The floor of the diencephalon in fishes is strongly developed in the form of the *inferior lobes*, structures which probably compensate in some degree for the imperfectly developed cerebral lobes of these forms.

The *diocœle*, or third ventricle, it will be recalled, is the deep, narrow cavity of the diencephalon between the walls formed by the thalami. It becomes shallower behind, while in front it is bounded by the *optic chiasma* and the *lamina terminalis*, the latter of which marks the true anterior end of the brain in the median line, and from which the cerebral hemispheres, budding out on either side extend forward secondarily, and laterally.

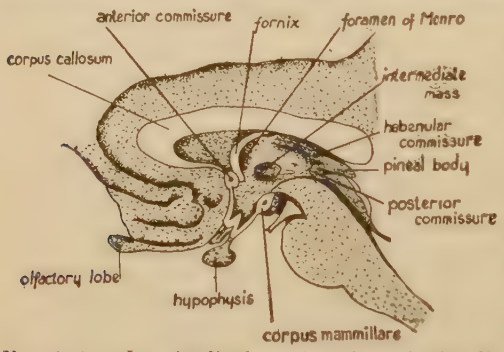


Fig. 581. — Longitudinal section through the diencephalon. (After Villiger-Piersol.)

There are three commissures in the diencephalon, (1) the *anterior*, joining the habenular centers on the two sides; (2) the *middle commissure*, formed as the result of union of the mesial surfaces of the thalami; and (3) the *posterior commissure* of medullated fibers, on the posterior wall of the diocœle above its entrance to the mesocœle, or the aqueduct of Sylvius (Fig. 581).

E. Telencephalon

As already pointed out, the true, median, anterior end of the brain is the *lamina terminalis*, or transverse wall that determines the anterior limits of the diocœle. From the lateral alar region on either side of this terminus grow out, both forward and backward, the *cerebral hemispheres*, which assume greater and greater importance throughout the vertebrate series, until in man they overshadow in size, complexity, and function, all other parts of the brain.

In fishes the cerebral development of the brain is hardly more

than a prophecy of what is to come, and even in amphibians the cerebrum is connected by communicating fibers only as far back as the diencephalon. This connection is extended to the mesencephalon in the reptiles and birds, while in mammals it reaches to the cord finally dominating the entire nervous system. The dominance of the cerebrum accordingly takes place gradually and may be said to be acquired somewhat at the cost of the posterior parts of the brain.

The floor of each half of the telencephalon consists largely of the *corpus striatum*, situated directly in front of, and continuous with, the thalamus, while the roof and sides form the *pallium*, which, in lower vertebrates, is a thin non-nervous wall inclosing the telocœles, or lateral ventricles, and becomes the foundation upon which the enormous cerebral cortex of higher vertebrates develops.

The corpus striatum receives its name from the fact that it consists of gray nuclear masses, "striated" with sheets of white medullated fibers, that form a conduction highway to and from the cortex. Where the cortex is poorly developed, as in reptiles and birds, the corpus striatum is an important reflex center in which correlation and coördination are effected. In fishes and amphibia without any cortex, the integrating center is situated farther back in the optic lobes of the mesencephalon.

The gray matter of the corpus striatum, located internally, takes the form of two central masses, the *caudate* and *lentiform nuclei*, so called because of their shape.

Originally, the telencephalon was very largely an olfactory organ, or "smell brain," with the thalami of the diencephalon serving as the "sight brain." Later during the course of the evolution of the brain, the sight center became more and more relegated to the mesencephalon, while the smell area, or *rhinencephalon*, diminished in size and importance until in man it is relatively insignificant, as shown by the very small olfactory lobes.

The original olfactory part of the pallium is termed the *archipallium*, while its anterior and lateral regions, which become the cerebral cortex in higher vertebrates, crowding the olfactory lobes down into an antero-ventral position, together are termed the *neopallium*, because of their more recent phylogenetic appearance. Among mammals the archipallium reaches its highest development in the marsupials, while the neopallium is best differentiated in man.

The size of the archipallium, as would be expected, is closely correlated with the sense of smell, being large and conspicuous in keen-smelling land animals, such as armadillos and hedgehogs, for example, and absent in the ocean-going dolphins.

The olfactory region of the telencephalon involves not only the *olfactory lobes* but also the *olfactory stalks*, which terminate in *olfactory bulbs* in some forms (Fig. 582). The *olfactory nerves* extend either directly to the lobes, or through the stalks and bulbs, when these are present, to the lobes from the mucous membrane of the nasal pits where the sense receptors of smell are located.

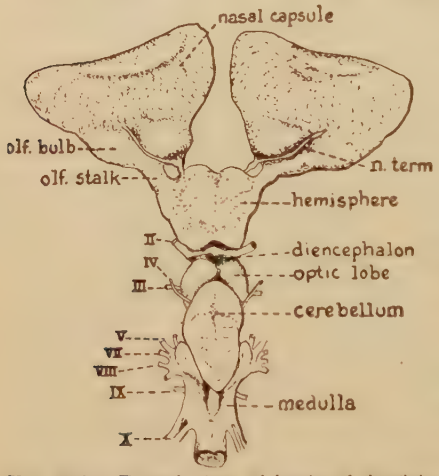


FIG. 582.—Dorsal view of brain of dogfish, *Galeus canis*, showing *Nervus terminalis*. (After Locy.)

Three pairs of prominent nuclei in the olfactory area, *lateral*, *medial*, and *intermedial*, relay the sensations received from the sense organs back to the mammillary bodies of the hypothalamus and to the habenular nuclei of the epithalamus, whence by another synapse they reach the crura cerebri of the mesencephalon and perhaps even more posterior parts of the brain.

The *telocœles* which form the brain cavities of the cerebral lobes, may extend even into the olfactory lobes, where they are properly called *rhinocœles*.

The neopallium, or non-olfactory part of the pallium, becomes overspread by the *cerebral cortex*, which in mammals is the great correlation and coördination center of the whole nervous system. The outer layer of the cerebrum is made up of gray matter, but its outstanding thickness is mostly due to white fibers immediately beneath the gray layer. These white fibers form an intra-mural network of great complexity, connecting different regions of the cortical area and forming a unifying or integrating organ of the greatest importance. As has been aptly said: "When we wake in the morning the sheet of gray cortex on the brain be-

comes the screen on which is lit up the cinema of the outside world." (Keith.)

In fishes and amphibia the gray matter of the brain, as of the cord, is arranged primarily inside, next to the ependymal lining of the ventricles, with the white conduction tracts outside. A second zone of gray matter begins to develop in reptiles and birds nearer the surface and considerably removed from the cavities of the brain. In mammals this zone becomes the gray cortex that covers the outside of both the cerebellum and the cerebrum.

The two hemispheres of the cerebrum, like kernels in a walnut, are connected with each other by commissures. Of these, the *anterior commissure* crosses from one side to the other in the lamina

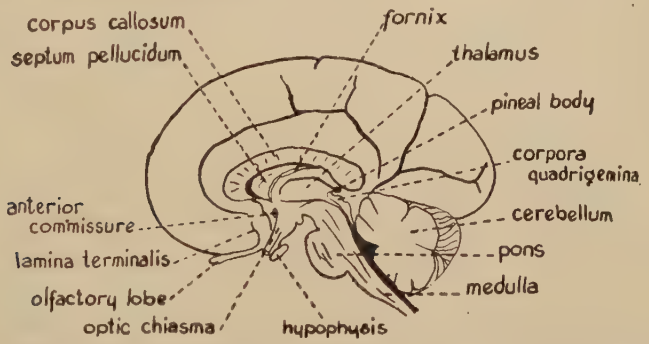


FIG. 583.—Median section through the human brain. (After Piersol.)

terminalis, while the *hippocampal commissure* is more posterior and ventral in position. The *corpus callosum*, a flattened arch of white fibers between the hemispheres and the largest of these commissures is plainly seen when the brain halves are severed from each other sagittally (Fig. 581). The anterior and hippocampal commissures connect the archipallial parts of the cerebrum. The corpus callosum unites the non-olfactory neopallial regions of the hemispheres.

Along the boundary between the thalamus and the cerebrum is the curved margin of the hemispheres, that becomes thickened into a white band of medullary fibers, called the *fornix*. Between the fornix and the corpus callosum is the thin *septum pellucidum* (Fig. 583), separating the two lateral telocœles and enclosing between its double walls a space, called the "fifth ventricle," which is not in connection with the rest of the ventricular cavities of the brain, being quite independent of them.

In most mammals, particularly the larger ones, the cortical surface of the hemispheres is further increased by the formation of folds or convolutions. The miniature mountain chains thus formed are called *gyri*, and the valleys between are termed *fissures* and *sulci* (Fig. 584). Such mammals as present these modifications have the sulci and gyri already marked out at birth. "The attempt to make a great deal out of this feature yields but little comfort" (Stiles), as the sheep and cow have deeply furrowed cortical surfaces, while some apes, with much more intelligence, have nearly smooth brains. In spite of the prevalent opinion to the contrary, the gray matter of the cerebrum, which is spread out over the irregular surface of the gyri and sulci, is not so much an index of intelligence as the subcortical white fibers, which bring about innumerable conditioned reflexes that transform the cerebrum into an effective organ of integration.

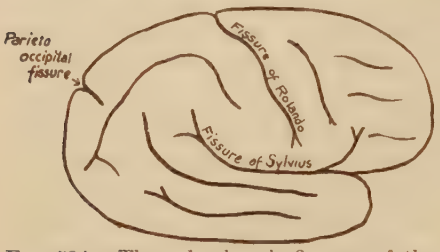


Fig. 584.—Three landmark fissures of the human cerebrum.

The sulci do serve, however, as boundary lines to certain arbitrary regions into which the cerebrum may be parceled out topographically for convenience in localization and description as the *frontal*, *parietal*, *occipital*, and *temporal lobes*, corresponding roughly to the cranial bones which cover them, besides the ventro-anterior *olfactory lobes* already mentioned. In addition to these lobes, which are all visible

Fig. 585.—Horizontal section through the hemispheres of the cerebrum. *1,2*, longitudinal fissures, the former between the frontal lobes, the latter between the occipital lobes; *3*, anterior part of the corpus callosum; *4*, the fissure of Sylvius; 5, Island of Reil; 6, caudate nucleus of corpus striatum; *7*, lenticular nucleus of same; *8*, optic thalamus. (From Dearborn, after Dalton.)

externally, there is also at the bottom of the deep *fissure of Sylvius* (Fig. 584), on either side, an important lobe called the *Island of Reil*, which is a point of origin that was once on the surface of the cerebrum, but later became overgrown by neighboring parts, like an upholsterer's button, drawn down into, and partially covered by, the surrounding cloth (Fig. 585 in black).

6. Cerebral Localization

A century ago Goll and Spurzeim attempted to associate certain human faculties with definite areas of the cortex. What began on their part as a legitimate scientific inquiry and experiment soon developed into the quagmire of *Phrenology*. This pseudo-science gained great temporary vogue in the hands of clever charlatans who knew very little about the brain. Trading upon the ignorance of the general populace, the wandering "Professors of Phrenology," by skillful guesswork and owlish digitation of "bumps" on the cranium, covered their lack of knowledge of cerebral localization, and were usually able to satisfy credulous mankind as to the hidden capacities of any particular brain. Thus "mute inglorious Miltons" and unrecognized rural Napoleons were discovered at fifty cents a head! Today the discredited phrenologist properly belongs with the witch doctor, medicine man, astrologer, clairvoyant, and fortune teller, but it must be admitted that many of his blood relatives, who would seek a quick short cut to the truth, which may only be gained by slow patient travel along a long road, are still abroad and active in various guises.

Modern science does not recognize the brain as a phrenological cabinet of pigeonholes in which separate "faculties," such as "generosity," "secretiveness," "amativeness," "philoprogenitiveness," and the like, are separately stored away, but rather as a vast clearing house of reflex arcs, not fundamentally different, except in complexity, from other reflex arcs of the nervous apparatus.

There is, however, a real localization of certain different functions in the cortex. This fact has been abundantly demonstrated both clinically and experimentally, as well as by the examination of brain lesions and defects in autopsies following various types of paralysis. One of the first proofs of cortical localization was furnished during the Franco-Prussian war in 1870, when two surgeons, Fritsch and Hitzig, operating upon a wounded soldier, demonstrated a definite localized muscular response when a certain

area of the exposed cerebrum on the opposite side was subjected to a slight galvanic stimulation.

The map of the brain, shown in Fig. 586, combines some of the discoveries that have been made of scientific cortical localization, as contrasted with the fanciful unscientific localization upon which phrenology was based. It will be noted that the nodal points there shown do not represent mental characteristics, or "faculties" at all, but are centers of association and projection in direct relation to external sense organs and effectors.

The phenomena included under the term *aphasia*, which may be manifested either as the loss of the power of speech, of the ability to comprehend spoken words, or to understand printed or written language that was formerly understandable, are found to be associated with lesions or defects in definite regions of the cerebral cortex.

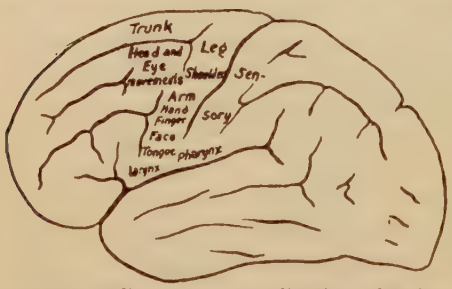


FIG. 586.—Cerebral localization, showing chief regions of the motor center. (After Piersol.)

The localized functional centers of the cerebrum, it should be added, shade into each other, like the distribution of the buildings of neighboring cities, and are not clearly delimited from each other. Thus, there are sensory centers of sight, smell, hearing, and cutaneous sensations, as well as various motor centers, that control movement of definite parts of the body. As would be expected, the cortical field for the facial muscles of an elephant, with its large trunk, is relatively much greater than the corresponding area in the rhinoceros.

7. The Control of the Body by the Brain

Animal activities, having their physical basis in the brain, are of three general categories, namely:

1. *Innate stereotyped functions*, which are inherited, and which are ordinarily blanketed together under the term *instinct;*
2. *Habits*, which are not inherited, but are patterns of conduct acquired by repetition until they become secondarily more or less automatic;
3. *Variable, modifiable actions*, which are marks of *intelligence.*

Of innate stereotyped functions it may be said that they do not lend themselves to individual improvement. It is futile, for example, to try to teach a grasshopper either to jump or to dance. It jumps already, having been born an instinctive jumper, and it can never learn to dance, since the "variable, modifiable" capacity is practically wanting in its make-up.

With an increase of cerebral function the instinctive reflexes take more and more to the background, and therein is the great distinction between "lower" animals, which are largely at the mercy of their environment and heredity, and the "higher" animals, which to an increasing degree have risen above the enviroring conditions and have become more and more "the captains of their souls." The most prized possession of mankind is the "capacity for individuality," yet even what passes for "free will" has its basis in the neurones and reflexes built up in the brain, that after all must be regarded as the mechanism *through which* consciousness, memory, imagination, and will are effected, rather than as the seat of these manifestations of the intellectual life.

The control which the brain, and particularly its cerebral part, exercises over the body, is increasingly greater as one passes from fishes to mammals. A frog, for instance, can recover from a surgical operation entailing the loss of the entire brain. Such a "spinal frog" continues to perform many of its functions in a practically normal fashion. A hen with its head cut off continues to flop about for some time but not so a mammal that has been guillotined, while in man a comparatively slight interference with even a minute portion of the cortex may result in sudden fatal apoplexy.

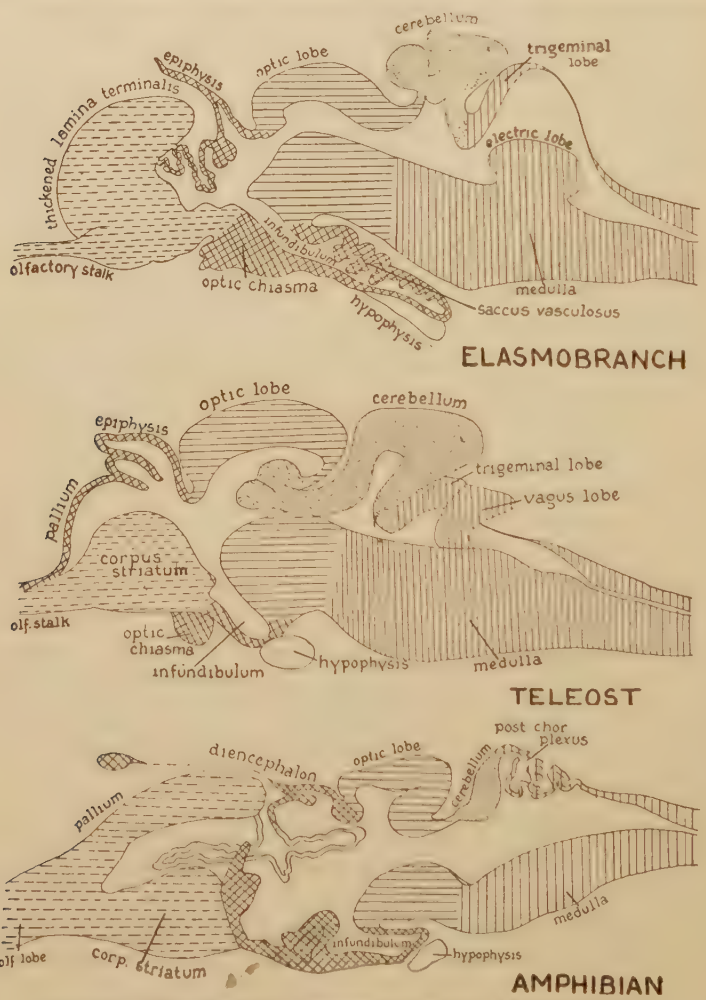
8. The Comparative Anatomy of the Brain

The essential features in the comparative anatomy of the vertebrate brain may be passed in review by an examination of the diagrammatic pictures of the brains of typical vertebrates, shown in Figs. 587–592.

A. Cyclostomes

The brain of the lamprey eel (*Petromyzon*) is primitively horizontal without flexures, and quite embryonic in appearance, with a long cordlike medulla, and a rudimentary liplike cerebellum. The saccus vasculosus, characteristic of fishes generally, is large, but the hypophysis is small. On the opposite or dorsal side of the

diencephalon, the pineal-parietal complex is represented by a well developed *pineal organ*, or *epiphysis*, with a projecting stalk, and located beneath it is a smaller *parietal*, or *parapineal* structure.



FIGS. 587–589. Sagittal diagrams of brains. (After Edinger.)

These two organs, arising from a common origin, were probably originally paired, since the pineal body is in intimate relation with the right, and the parietal body with the left, habenular ganglion. The presence in certain fossil fishes, for example, *Titanichthys*,

of a pair of foramina located side by side in the skull directly above this region of the brain, seems likewise to point to the originally paired relation of these organs. The tandem-like position of the pineal and parietal bodies in cyclostomes, is apparently the result of a secondary displacement. The histological structure of the pineal organ, as well as its access to light through a foramen in the skull covered over by a transparent skin, seems to indicate that the pineal body in cyclostomes is a photoreceptive organ by means of which light and darkness at least may be distinguished.

No differentiation takes place in the corpus striatum, only an olfactory archipallium being developed. The hemispheres of the telencephalon are to be interpreted as olfactory lobes posteriorly with somewhat larger olfactory bulbs anteriorly, separated by a slight constriction.

The brain of the hagfishes, for example, *Myxine*, apparently differs to quite an extent from that of the lamprey eels, since it seems to have undergone a certain degree of retrogressive adaptation in connection with its parasitic method of life. The anterior end is broader and plumper, as the suctorial habit of the hagfishes would demand, and both the saccus vasculosus and the chorioid plexus, along with the ventricles of the brain, are much reduced. The cerebellar lip also, which is laid down normally in embryonic life, later disappears entirely.

B. Elasmobranchs

The brain of elasmobranchs, (Fig. 582), differs from that of other fishes in the greater elaboration of the telencephalon and cerebellum, and in the relatively larger medulla. There are pronounced differences, as would be expected, between the active sharks and dogfishes, and the sluggish skates and rays, the cavity of the cerebrum and the accompanying anterior chorioid plexus, for example, being obliterated in the *Myliobatidæ*.

The bulging corpora striata, and the dominant olfactory lobes, constitute the bulk of the telencephalon, while the incipient hemispheres, which are incorporated inseparably with the archipallial olfactory area, are separated from each other by only a slight intercerebral fissure.

From the olfactory lobe there extend forward two conspicuous olfactory tracts, terminating in olfactory bulbs, which are frequently larger than all the rest of the telencephalon. The ol-

factory tracts in certain elasmobranchs, such as *Hexanchus* and *Myliobatis*, may exceed the entire median length of the brain.

In the diencephalic region the epiphysis is stalked, reaching sometimes as far as the cartilaginous roof of the cranium. The parietal organ, after temporary appearance during embryonic development, disappears. Prominent *inferior lobes*, on either side of the hypophysis, are present on the floor of the diencephalon.

The well developed optic lobes in the mesencephalon are partially covered over by the forward growth of the large cerebellum, which is somewhat folded and marked off dorsally into four conspicuous areas.

In the antero-lateral region of the medulla are prominent *restiform bodies*, standing out laterally on either side of the cerebellum with which they are in intimate morphological and functional relationship.

The electric *Torpedo* shows two *electric lobes* (Fig. 587), that project forward from the anterior floor of the myocœle. These are regarded as the hypertrophied nuclei of the Xth (vagus) cranial nerve.

C. Other Fishes

The variation in the brain of fishes, other than cyclostomes and elasmobranchs, is so great that a composite picture is difficult to draw. Some features, however, are said to be in general, characteristic.

Usually the fish brain does not entirely fill the cranial cavity. There is still "room to let" in spite of the fact that the cranium and its cavity make up only an insignificant part of the entire skull.

The pallium, or roof of the telencephalon, is thin and nonnervous (Fig. 588). The convex corpora striata, which occupy the floor of this region, might easily be mistaken by the superficial observer for the cerebral lobes. There is no cerebrum present.

The epiphysis, with a shortened stalk, is on the road to degeneration, and does not ordinarily reach upward as far as the skull, although it is well developed in certain deep-sea fishes.

The optic lobes of the mesencephalon reach their highest development in teleost fishes, sometimes becoming larger than all the rest of the brain together.

The cerebellum usually grows backward like a tongue over the anterior region of the medulla, more rarely extending forward, like the elasmobranch cerebellum, and encroaching upon the large optic lobes.

Its size is correlated closely with the swimming ability of the animal in question, being relatively small in the sea horse (*Hippocampus*) and the flatfishes (*Pleuronectidæ*), for example, but much larger in the flying fish (*Exocœtes*) and such famous travelers as the eel (*Anguilla*).

While the various classes of fishes as a whole exhibit brains representing side alleys in evolutionary progress, the rare lungfishes (*Dipnoi*), offer certain prophetic modifications that perhaps foreshadow the brains of higher vertebrates. Olfactory stalks are dispensed with, the corpora striata assume a less prominent rôle, and cerebral hemispheres, the thickening walls of which are supplied with hopeful neurones, are initiated.

The cerebellum, when contrasted with that of the more active elasmobranchs, however, appears to have lost much of its prominence. Embryonic rhinocœles are present in the olfactory lobes, and, in Protopterus, at least, the pineal body shows a primitive condition by extending even as far as a foraminal window in the roof of the skull.

D. Amphibians

In amphibians (Fig. 589), the large elongated olfactory lobes, which are continuous with the distinctly separated cerebral lobes, lie closely side by side, and are joined together medially.

The corpora striata project upward from the telencephalic floor only slightly, allowing for fairly large telocœles and an invaginated anterior chorioid plexus inside of the cerebral lobes. The latter are without an external layer of gray matter, although scattered neurones begin to appear in the pallial wall.

The diencephalon is uncrowded and externally visible, without inferior lobes, but with a generous *optic recess* in front of the hypophysis in the infundibular region. In adult anurans the epiphysis is represented by a small median vesicle close under the dorsal wall of the cranium, which, by its development, is shown to be the bulbous tip of the vanished stalk of the epiphysis. The skulls of extinct *Stegocephali*, a group commonly reckoned as amphibians, show a dorsal foramen, which records the former

presence of either a pineal or a parietal organ in this region. There is no parietal body in modern Amphibia.

The optic lobes have been spread so as to occupy a more lateral position, and the cerebellum, reduced to a transverse lip in most forms, is quite rudimentary in the Apoda and some newts, for example, *Proteus*.

The brain of the elongated urodeles, which more nearly resembles that of the dipnoans than of other fishes, is perhaps the most schematic in structure of any vertebrate brain.

E. Reptiles

The reptilian brain (Fig. 590), shows an advance in the telencephalic region, since a gray cortex, although not pronounced, is definitely laid down, and the commissures between the cerebral lobes are more in evidence than in the amphibian brain.

The corpora striata are so large that only small telocœles remain, but rhinocœles extend into the olfactory lobes. In most reptiles the olfactory lobes are closely applied to the hemispheres and are not externally visible, but in those lizards and alligators with prominent projecting snouts, the olfactory lobes are prolonged into tracts and bulbs, as in the elasmobranchs.

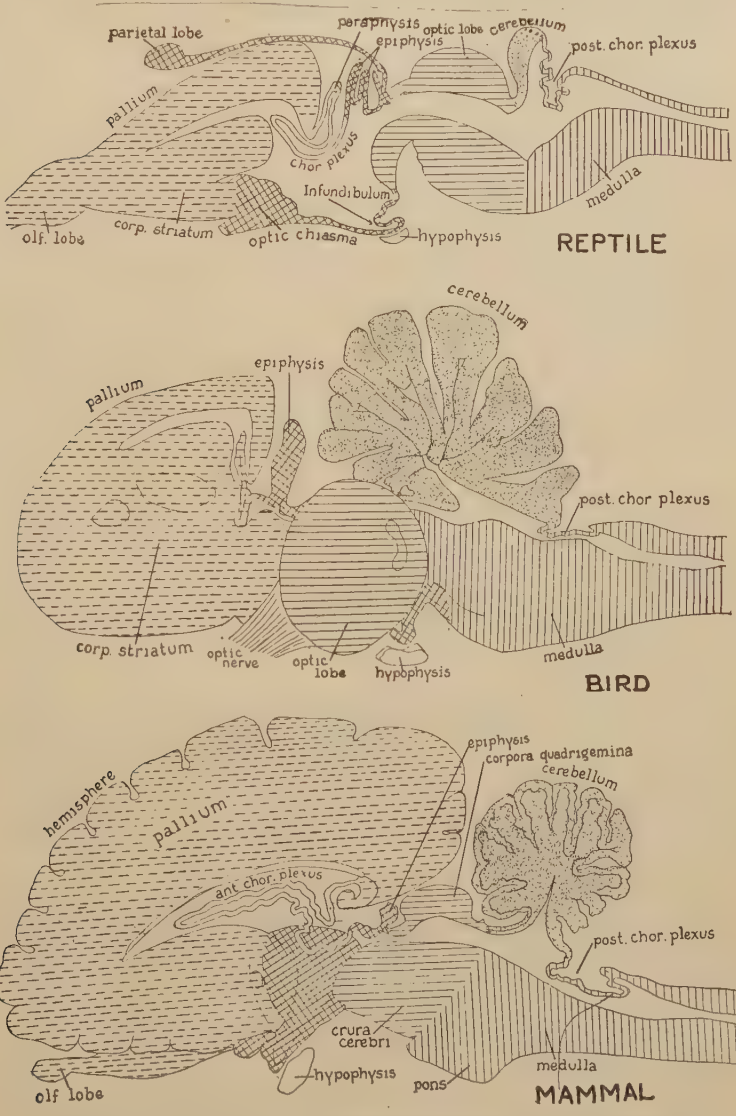
The diencephalic region of the brain of reptiles is of particular interest. The thalami are large, while the hypophysis, of double origin, is definitely differentiated into an anterior and a posterior part, the former enveloping the latter, which is hollow and in communication with the infundibulum. There is no saccus vasculosus.

On the thin dorsal wall there are always present, at least embryonically, not only pineal and parietal bodies, but also a third evagination, the *paraphysis* (Fig. 413), which is so far anterior in position that it may be said to belong to the telencephalon. The function of the paraphysis, which usually undergoes degeneration in adult life, is unknown.

Except in the Crocodilia, the epiphysis is always present as a glandular structure. The parietal organ also, which is closely associated with the same ganglionic supply as that of the pineal body, is always present, reaching its highest development in the reptiles. In *Sphenodon* particularly, the parietal organ is unmistakably a median eye, equipped with a retina and a lens, and reaching through the top of the skull.

F. Birds

The brain of birds (Fig. 591) is more an "eye brain" than a "smell brain," thus showing an advance over its forerunners. The olfactory lobes, which are fairly well developed in the tooth-



Figs. 590–592.—Sagittal diagrams of brains. (After Edinger.)

bearing Cretaceous birds, are small and degenerate in modern birds, while the gray cortex of the cerebrum, being confined to a small posterior part of the hemispheres, shows little advance over that of the reptiles, owing to the enormous development of the corpora striata with which the anterior half of the pallium becomes fused. The telocœles are thus reduced to very restricted spaces.

There is no trace of a parietal organ in birds, and the degenerate pineal body is buried between the encroaching cerebrum and cerebellum. In fact the whole brain of the bird gives the impression of crowding and centralization, characteristic of the bird's structure generally. This is due not only to the fact that the optic lobes are crowded over laterally in position, but also to a considerable backward growth of the cerebral lobes, and a corresponding forward growth of the cerebellum, which tends to bury the diencephalon and mesencephalon from dorsal view.

The cerebellum proper exhibits a well defined median *vermis*, so called from its fancied resemblance to an annelid worm, as well as two lateral *flocculi*, which adorn the sides of the vermis.

G. Mammals

Tertiary mammals, as methods of exploring the cranial cavity of fossil skulls reveals, had a reptilian type of brain. In modern mammals also, the brain (Fig. 592) is more like that of reptiles than of birds, since the outstanding size of the cerebrum is due to a development of the cortex rather than to enlarged corpora striata, as is the case among birds.

The commissural systems between the cerebral lobes are better developed than in other vertebrates, particularly by the elaboration of the large corpus callosum, although this is lacking in the monotremes and marsupials, where the anterior commissure may be regarded as its precursor.

While still quite prominent in the primitive edentates, the archipallial olfactory part of the brain is still more reduced among higher mammals, until in man it becomes very small, and in seals and whales is almost entirely lacking. Usually there are no rhinocœles in mammalian olfactory lobes, although these occur in certain perissodactyls.

The cerebrum is without convolutions in *Ornithorhynchus*, most marsupials, many rodents, and also in insectivores and bats. When

present they are better developed in large-bodied animals, such as cattle and elephants, than in smaller mammals.

In the diencephalon the thalami are large, and the hypophysis is attached to the infundibulum to form a compound endocrine organ. The epiphysis, which has also become possibly changed over to endocrine activity, has lost its original eyelike structure, being reduced to an organ degenerate in size, although indispensable in function. It is usually covered over by the hemispheres, and is relatively large in ungulates and rodents, but missing in armadillos and other edentates.

The two optic lobes of lower forms become changed in mammals into four corpora quadrigemina, which are relatively smaller than is this region of the mesencephalon in any other vertebrate, and are quite covered by the massive cerebral lobes.

The cerebellum is not only divided antero-posteriorly into anterior, median, and posterior regions, but has also inserted laterally between the vermis and the flocculi two cerebellar hemispheres, that although small in the lower mammals, attain considerable size in the higher mammals and eventually make up the bulk of the cerebellum.

A further characteristic of the mammalian brain is the pons, which may be described as a definite band of fibers encircling the brain stem in the metencephalic region.

The medulla of mammals is comparatively short, and appears to be drawn under the prominent cerebellum.

9. The Weight of the Brain

The average weight of the brain of a Caucasian male is about 1360 grams, or 48 ounces. Notable exceptions on record are that of Thackeray, the novelist, 1644; of Cuvier, the naturalist, 1830; of Döllinger, the anatomist, 1207, and of an Australian bushman, 1185.

The weight of the brain of a dog, gorilla, and man having approximately the same weight of body, has been found to be 135, 430, and 1350 grams respectively. The absolute weight of the brain, however, is not in itself a reliable criterion of intelligence, since various factors, such as age, sex, form of skull, and weight of body, as well as the comparative size of different parts of the brain, must be taken into account. The cerebral hemispheres of the rabbit, for example, constitute something more than half the

bulk of the entire brain, while in man the cerebrum exceeds four-fifths of its total weight.

The actual mass of the human brain is only exceeded among living animals by that of elephants and whales, the size of whose body is many times that of man.

An examination of the cranial cavities of the gigantic reptiles of the Mesozoic age, reveals the fact that they had insignificant brains in proportion to the enormous bulk of their bodies. Indeed it is a source of astonishment that these monsters of the past were able to get about with brains relatively so small, but it must be remembered that eventually they did succumb after an evolutionary experiment of several million years. It is doubtless more than a coincidence that the twilight of the dinosaurs and their reptilian contemporaries fell at about the same time as the sunrise of the mammals, who were at first comparatively insignificant in size, but who had a new revolutionary ratio established between weight of the brain and weight of the body.

IX. PERIPHERAL NERVOUS SYSTEM

An indispensable auxiliary of the central nervous system is the *peripheral nervous system*. This consists of *nerves*, or free conductors, which put end organs into physiological connection with their centers, as distinguished from *nerve tracts*, or communicating fibers embedded within the cord or brain itself. Nerves extend through mesenchymatous tissues to all parts of the body, and although their number is not large primarily, the neurones, or morphological nervous elements which combine to make the cable-like nerves, (Fig. 593), may number, according to Donaldson, as many as three or four millions in man.

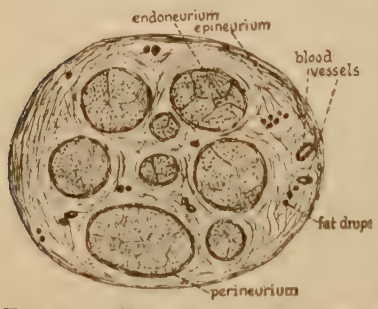


FIG. 593. Cross section of a human nerve. (After Quain.)

The nerves associated with the central nervous system are in pairs, and are either *spinal* or *cranial*, according to their connection with the cord or the brain. The additional *involuntary*, or *sympathetic nervous system*, attends to many necessary reflexes without involving the central system, just as an efficient office

boy disposes of many time-consuming intruders without disturbing the general manager, who is supposed to be engaged in more important business in the inner office.

1. Spinal Nerves

In man there are typically 31 pairs of spinal nerves, as follows: cervical, 8; thoracic, 12; lumbar, 5; sacral, 5; caudal, 1. The total number of spinal nerves in vertebrates other than man, is naturally subject to wide variation.

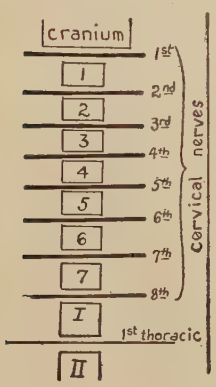


FIG. 594. — Diagram showing the relation of the cervical nerves to cervical vertebræ.

Each pair of spinal nerves, with the exception of the cervical, takes its name from the vertebra just anterior to its exit. The reason for a reversal of designation in the cervical nerves, is that the first pair emerges between the skull and the first cervical vertebra, or atlas, and so, having no vertebra in front of it, takes its name from the one immediately behind it. Since this method of nomenclature is followed throughout the cervical series, the last pair of cervical nerves is left without any vertebral godfather standing behind it, and is accordingly called the eighth cervical pair, while the next pair that plainly belongs to the body and not to the neck, is named the *first thoracic pair*, with reference to the vertebra *behind* which it emerges (Fig. 594).

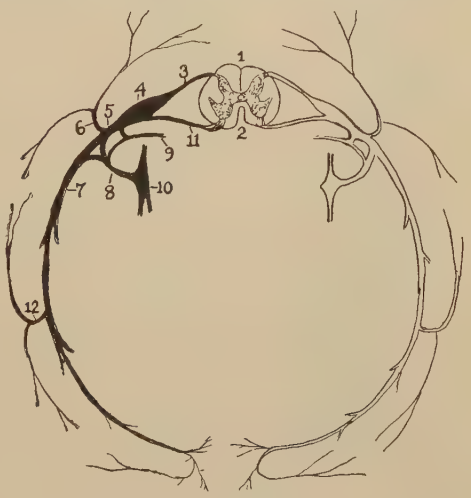


FIG. 595. — Cross section of the central and peripheral nervous systems in man. *1*, dorsal fissure of nerve cord; *2*, ventral fissure; *3*, dorsal root; *4*, dorsal ganglion; *5*, spinal nerve; *6*, dorsal branch; *7*, ventral branch; *8*, ramus communicantes; *9*, meningeal branch; *10*, sympathetic ganglion; *11*, ventral root; *12*, cutaneous branch. (After Rauber.)

The size of the spinal nerves is dependent upon the relative area of the body which they supply, the largest in man being the first sacral pair that supplies the legs.

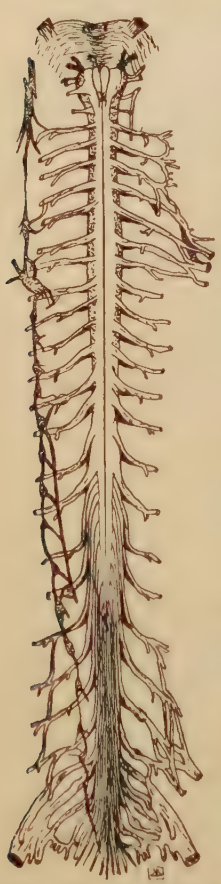


Fig. 596.—The spinal cord of man, showing plexi, the *cauda equina*, and on one side, the sympathetic nerve chain. (After Rauber.)

The general distribution of the spinal nerves, with the regions which they supply in man, is indicated in Fig. 595. The relation between the spinal nerves and the metameric embryonic muscles is very regular, but the rearrangement and migration of these muscles in the adult organism, brings about an apparent irregularity. A nerve once associated with a muscle, however, remains faithful to it throughout all its subsequent transformations, as is well illustrated by the innervation of the diaphragm which, being derived from myotomes formerly located in the neck region, is effected by a branch of a cervical nerve, the *phrenic nerve*, that is drawn out of its way for a considerable distance, at the same time retaining its original relationship.

The fact that metameric muscles do not extend as myotomes to the tails of mammals, as in the case of fishes and urodeles, accounts for decided differences in the abundance of postanal spinal nerves in the higher and lower vertebrates.

In man particularly the nerve cord is shortened, as already described (p. 598), so that it does not extend through the entire length of the vertebral column, nevertheless the emerging spinal nerves maintain their proper exits. This necessitates the continuation of the posterior pairs of spinal nerves for increasingly lengthened distances within the neural arch of the vertebral column before they finally emerge, with the result that a brush of spinal nerves, the *cauda equina*, is formed at the end of the cord (Fig. 596). Moreover, while the anterior spinal nerves leave the cord at practically right angles, the angle of departure for posterior pairs becomes more and more acute, until it may

be said that the sacral nerves are for some distance almost or quite parallel with the *filum terminale*, or the non-nervous continuation of the cord itself.

A. Roots

The connection between the peripheral nervous apparatus and the central nervous system, is effected on either side through the dorsal and ventral *roots* of the nerves (Fig. 595). These roots differ not only in structure and function, but also in their origin and manner of development.

The *dorsal roots* are composed primarily of sensory neurones whose polarity is afferent, that is, towards the central system. The *ventral roots* are efferent, carrying messages outward to glandular or muscular effectors, and since these effectors, being mostly muscular, bring about motion, the ventral roots are commonly designated "motor" roots (Fig. 597).

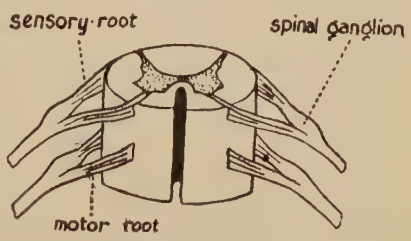


Fig. 597.—Diagram of the formation of spinal nerves. (After Piersol.)

In most cases the dorsal and ventral roots join to form a spinal nerve, which becomes in consequence a *mixed nerve*, or cable of both efferent and afferent neurones over which messages may pass in either direction.

From the point of junction of the two roots of a mixed nerve, four branches are given off, (1) a thinner dorsal branch; (2) a thicker ventral branch, supplying the skin and body musculature; (3) a small meningeal branch, going back to the meninges; and (4) a sympathetic branch, connecting with ganglia which relay to the viscera. All of these branches are mixed, and have, therefore, both kinds of neurones (Fig. 595). The important generalization that the branches of spinal nerves are mixed, while their roots are not, was independently established over a century ago by the Frenchman, Magendie, and Sir Charles Bell, an Englishman, who has been characterized by Professor Keith as "an anatomical detective of the highest rank."

For the most part the dorsal roots are made up of fibers from neurones that, although apparently unipolar are really bipolar, being located in the dorsal ganglia, the origin of which from the edge of the medullary groove has already been described.

The neurites of the ventral roots, on the other hand, proceed from neurones located in the ventral gray matter of the cord.

The visceral, or sympathetic branch contains elements whose neurones, efferent as well as afferent, are associated with the lateral gray area in the cord between the dorsal and ventral horns of gray matter. The visceral sensory and motor elements are thus associated with the lateral plate of gray matter in the cord, while the somatic sensory and motor components are connected with the dorsal and ventral horns respectively.

In the lower vertebrates dorsal roots are not always purely sensory, and a few recurrent sensory fibers may pass from the dorsal to the ventral root also, thus modifying the character of the motor roots.

In function the efferent neurones of the ventral root may exercise either an excitatory or an inhibiting effect upon the muscles or glands to which they extend, although the question of the inhibitory action of nerves is by no means a settled one. Sherrington has shown that for the skeletal muscles the inhibitory

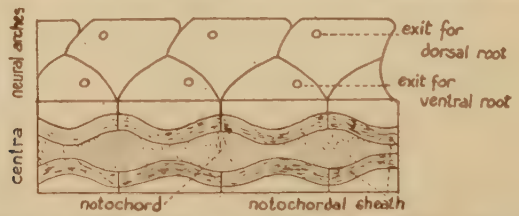


FIG. 598. Long section through a piece of the vertebral column of a shark, showing that the roots of the spinal nerves pass out diagonally with relation to each other.

mechanism is internal, that is, in the central nervous system, and consists of a block impulse that cuts out motor impulses and also tonus impulses.

The spinal nerves of amphioxus and the lamprey eel (but not of the hagfish), are either entirely efferent or afferent in character, since the sensory and motor roots do not join to form mixed nerves. The two-way mixed nerve, therefore, probably represents a secondary evolutionary adaptation and not a primitive condition.

The dorsal and ventral roots in elasmobranch fishes do not emerge from the cord in the same transverse plane, but alternate with each other before joining to form a spinal nerve (Fig. 598).

Dorsal roots make an intervertebral exit, while ventral roots come out vertebrally through foramina which penetrate the centra of the vertebræ. In higher vertebrates both roots of a spinal nerve emerge intervertebrally in the same transverse plane.

Also in fishes the dorsal ganglia and the union of the roots of the spinal nerves, are usually located outside the skeletal vertebral column, but in other vertebrates the junction is effected closer and closer to the cord itself, so that it comes to lie entirely within the neural arch (Fig. 599).

Fig. 599. — Diagrammatic section through a vertebra at the level of the roots of a spinal nerve, showing the position of the spinal ganglia with reference to the vertebra. (After Jammes.)

B. Plexuses

Whenever an extra large area, such as that of the arms or legs, is to receive a nerve supply, several spinal nerves may join forces, forming a *plexus*. A complication of this kind naturally adds difficulty to the precise tracing out of the sequence of neuronic lines between the central nervous system and specific end organs.

Fig. 600.—Diagram of the right brachial plexus in man, viewed from the front. The shaded strands are derivatives of the dorsal half of the plexus. *C*, cervical nerves; *T*, thoracic nerves. (After Eisler.)

The first four cervical nerves in man form the *cervical plexus*, supplying the neck, while the last four, together with the first thoracic nerve, make up the *brachial plexus* of the arm (Fig. 600). The other thoracic nerves do not enter into plexus formation, but all of the remaining *post*-thoracic nerves, that is, the lumbar, sacral, and caudal nerves, may become involved in the large *lumbosacral plexus*, which supplies the pelvic region and the leg.

In all of these plexuses it is the ventral, or efferent, roots alone that are concerned, since the dorsal sen-

sory roots remain independent of each other, although in fishes the dorsal as well as the ventral roots may anastomose.

In the case of long-bodied fishes and urodeles, which do not use their paired appendages for the support of the body, there is frequently, in different species, a shifting, anteriorly and posteriorly, along the backbone, of the girdles and their attached appendages, particularly the pelvic girdle, with a consequent variation in the group of spinal nerves that take part in plexus formation (Fig. 601).

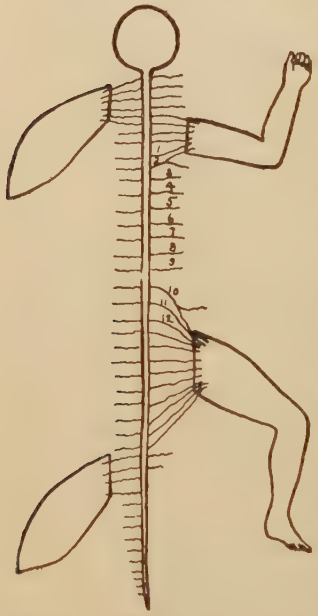


Fig. 601.—Diagrams of the relations of the appendages to the spinal nerves in fishes (left) and man (right). The nerves which supply the pectoral fin in fishes become the cervical nerves in man. The pelvic-fin nerves of fishes become the coccygeal nerves in man. The arm of man is supplied by the four posterior cervical and two anterior thoracic nerves, forming the brachial plexus. The pelvic plexus is made up of the 11th and 12th thoracic, and nine lumbar nerves. (After Wiedersheim.)

There are many variations in the composition of the spinal plexuses in other vertebrates, in which the legs and arms assume more importance, and the anastomoses may be unlike even on the two sides of the same individual.

Fig. 602. — Spinal nerves of a snake, in the pelvic region, showing a simple plexus in the absence of hind legs. (After Carlsson.)

As many as twenty-five spinal nerves may be fused together in the enormous brachial plexus of the skate, for example, while in certain other elasmobranchs as many as three cranial nerves even may join with spinal nerves to form a *cervicobrachial plexus*. In the long-necked swan the first spinal nerve to join with another in the brachial plexus, is the twenty-second.

Fig. 603.—The limbless embryo of a snake, 3.5 mm. in length.

A lumbosacral plexus in certain snakes (Fig. 602), in which

no trace of limb buds appears in the embryo (Fig. 603), indicates that these highly modified limbless reptiles were derived from ancestors with legs, at some time in the remote past.

2. Cranial Nerves

The cranial nerves are more specialized than the spinal nerves, as they have more differentiated tasks to perform, yet they bear an unmistakable resemblance to their spinal relatives, especially in the lower vertebrates. The differences which characterize cranial nerves depend largely upon (1) the degeneration, or suppression, of one or the other of the double roots; (2) the introduction of additional neuronic components not represented in spinal nerves; or (3) the hypertrophy or fusion of elements already present.

For example, in addition to the afferent somatic and visceral motor neurones of the ventral root, which are typical of the spinal nerves, there are present in cranial nerves three other types of neurones, namely, *special somatic afferent* neurones, and *special visceral afferent* neurones, both of which occur in direct relation to the superimposed cranial sense organs of sight, hearing, smell, and taste, and *special visceral efferent* neurones, that are associated with the branchiomeric musculature of the primitive gill arches and its derivatives. No single pair of cranial nerves possesses all of these seven functional types of elements, and no two pairs have the same composition, as will be evident from the inspection of the following *Table of Cranial Nerves* on pp. 648–9.

The sensory elements of cranial nerves, as in spinal nerves, are associated with ganglia located outside of the brain itself. The efferent motor elements, on the other hand, have their headquarters located within the substance of the brain.

The twelve pairs of cranial nerves were first identified in man, and are named with reference to the parts which they supply. They are customarily designated by the Roman numerals, I to XII. In the anamnia the last two pairs of cranial nerves (XI and XII), are outside the confines of the cranium and must be regarded as still spinal in character.

In certain fishes a group of small transitional *spino-occipital* nerves, numbering from one to five pairs, although spinal in character and not directly associated with the cranial nerves, have their origin within the skull. They wholly disappear in the Amphibia and higher vertebrates.

TABLE OF CRANIAL NERVES

NUMBER	NAME	SUPERFICIAL ORIGIN	COMPOSITION OF FUNCTIONAL COMPONENTS	POINT OF ORIGIN	TERMINAL SUPPLY
O	Nervus terminalis	Telencephalon	General somatic afferent	Cerebral hemispheres	Nasal septum
I	Olfactory	Telencephalon	Special visceral afferent	Olfactory mucous membrane	Olfactory bulb and lobe
II	Optic	Diencephalon	Special somatic afferent	Retina	Lateral geniculate body Pulvinar, superior colliculus
III	Oculo-motor	Mesencephalon	General somatic efferent	Oculo-motor nucleus	Extrinsic eye muscles, except IV and VI
			General visceral efferent	Edinger-Westphal nucleus	Ciliary ganglion and intrinsic eye muscles
IV	Trochlear	Anterior medullary velum	General somatic efferent	Trochlear nucleus	Superior oblique muscle
V	Trigeminal	Myelencephalon	General somatic afferent	Gasserian ganglion	Skin and stomodæal epithelium
			Special visceral efferent	Motor nucleus of V	Motor fibers to muscles of mastication
VI	Abducens	Myelencephalon	General somatic efferent	Abducens nucleus	Lateral rectus muscle
VII	Facial	Myelencephalon	Special visceral afferent	Geniculate ganglion	Taste-buds in anterior third of tongue
			General visceral efferent	Superior salivatory nucleus	Submaxillary and sublingual salivary glands
			Special visceral efferent	Motor nucleus of VII	Superficial face and scalp muscles, platysma, posterior belly of digastric, stylohyoid muscle

TABLE OF CRANIAL NERVES—*Continued*

NUMBER	NAME	SUPERFICIAL ORIGIN	COMPOSITION OF FUNCTIONAL COMPONENTS	POINT OF ORIGIN	TERMINAL SUPPLY
VIII	Acoustic	Myelencephalon	Special somatic afferent	Vestibular ganglion	Semicircular canals, utriculus, sacculus
				Spiral ganglion	Organ of Corti
IX	Glosso-pharyngeal	Myelencephalon	General visceral afferent	Petrosal ganglion	Pharynx and posterior third of tongue
			Special visceral afferent	Petrosal ganglion	Posterior third of tongue
			General visceral efferent	Inferior salivatory nucleus	Parotid gland
			Special visceral efferent	Nucleus ambiguus	Muscles of pharynx
X	Vagus	Myelencephalon	General somatic afferent	Jugular ganglion	External ear
			General visceral afferent	Nodose ganglion	Pharynx, larynx, trachea, esophagus, thoracic and abdominal viscera
			General visceral efferent	Dorsal motor nucleus of X	Thoracic and abdominal viscera via sympathetic ganglia
			Special visceral efferent	Nucleus ambiguus	Striated muscles of pharynx and larynx
XI	Spinal accessory	Myelencephalon	General visceral efferent	Dorsal motor nucleus of X	Thoracic and abdominal viscera via sympathetic plexus
			Special visceral efferent	Nucleus ambiguus	Striated muscles of pharynx and larynx
				Anterior gray column of cord	Trapezius and sternocleidomastoid muscles
XII	Hypoglossal	Myelencephalon	General somatic efferent	Hypoglossal nucleus	Musculature of tongue

Since the time of the identification of the twelve regular pairs of cranial nerves, the somewhat embarrassing discovery of an additional pair has been made. This is called the *Nervus terminalis* (Fig. 582). It was first found in the Dipnoi and is now known to be present, at least embryonically, in all classes of vertebrates, including man. As the Nervus terminalis is anterior to all other cranial nerves, it remains without a Roman numeral to characterize it, since its proper logical designation as the first pair would upset the well established and generally accepted succession of the other twelve pairs.

From the Table it will be seen that most of the cranial nerves take their apparent origin from the myelencephalon, or medulla (Fig. 573). The exceptions are the Nervus terminalis and the olfactory (I), which connect with the telencephalon; the optic (II) from the diencephalon; the oculo-motor (III) from the mesencephalon; and the trochlear (IV) from the region between the mesencephalon and the metencephalon.

Furthermore, as far as function is concerned, I, II, VIII, and probably the Nervus terminalis, are sensory in character, lacking motor roots, while III, IV, VI, and XII, having lost their sensory components, are entirely motor. The remaining pairs, namely, V, VII, IX, and XI, are reckoned as mixed nerves, although some of them have branches that are either all sensory or all motor in character.

With regard to neuronic components, the distribution is as follows:

	N. t	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
General somatic afferent	#					#					#		
General visceral afferent								#		#	#		
Special visceral afferent		#						#		#			
Special somatic afferent			#						#				
General somatic efferent				#	#		#						#
General visceral efferent				#				#		#	#	#	
Special visceral efferent						#		#		#	#	#	

The following brief survey of the cranial nerves supplements the information contained in the Table of Cranial Nerves.

A. Nervus terminalis (0)

The terminal nerve arises from the cerebral hemispheres in the region of the medial olfactory tract and extends to the nasal septum in close association with, but independent of, the olfactory nerve. It is without a medullary sheath, and is ganglionated and sensory. Its exact function is unknown. In elasmobranchs, where it is relatively larger than in other vertebrates, it extends to the olfactory mucous membrane.

B. Olfactory (I)

A peripheral ganglion, such as might be expected in a sensory nerve, is lacking in the olfactory. It is an unmedullated nerve, consisting in fact of neurites proceeding from cells located in the mucous membrane of the nasal pit, which constitutes the sense organ of smell. These neurites do not have far to go to reach the olfactory lobe of the brain by synapse via an olfactory bulb or tract, when present, or directly, when these structures are absent.

In the skull of most vertebrates the olfactory nerve passes through a single foramen on either side to reach the brain, but in many of the higher mammals it consists of a bundle of non-medullated fibers, *fila olfactoria*, which separately penetrate the skull through the pepperbox-like pores of the cribriform plate of the ethmoid bone. Thus, in man, instead of a single pair of olfactory nerves it would be more correct to say that there are at least twenty pairs.

C. Optic (II)

Like the olfactory nerves the optic nerves are not nerves at all, in the sense of arising from dorsal ganglia, or growing out from nuclei within the brain. They are rather backgrowths from a portion of the brain itself, the wall of which has grown out on either side from the main part, early in embryonic life, forming two optic stalks. After evaginating thus from the lateral walls of the diencephalon, the hollow bulbs at the ends of these stalks cave in, making double cups, in the inner walls of which neurones eventually differentiate, forming chains of retinal cells that extend back along the optic stalks to the brain, thereby making up the optic nerves. Upon reaching the brain on the ventral side at the boundary between the telencephalon and the diencephalon, the mass of fibers making up the optic nerves crosses over to the opposite side before penetrating further into the more posteriorly located

sight centers of the brain. This crossing of fibers forms the *optic chiasma*, which, in cyclostomes, elasmobranchs, ganoids, and dipnoi, is inconspicuously embedded in the brain, but in other vertebrates is plainly visible, and may even interlace in quite a complex manner. Among higher primates, including man, the chiasma is not complete, many fibers remaining on their own side

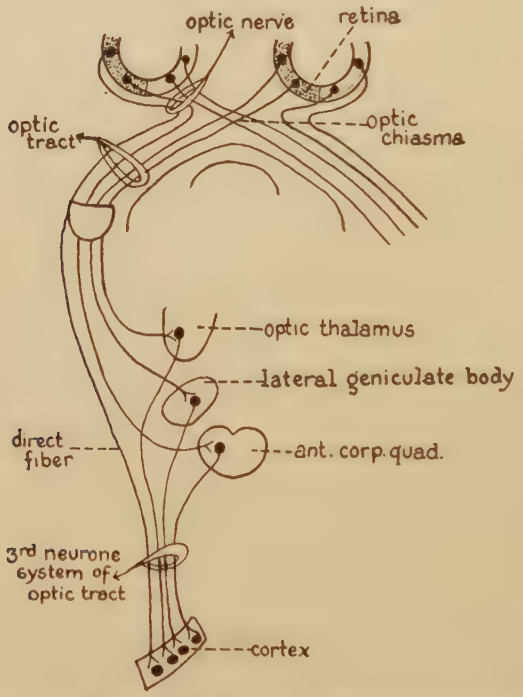


FIG. 604.—Human chiasma and nerve tracts associated with sight.

(Fig. 604), a condition which probably has something to do with the binocular method of vision, characteristic of higher primates.

D. EYE-MUSCLE NERVES (III, IV, VI)

The nerves of the eyeball muscles have much in common, all being originally somatic, or efferent nerve roots without sensory elements, growing out from the basal-plate region of the brain.

The most important of these is the *oculomotor* (III) which supplies not only the inferior oblique and three of the rectus muscles, namely, superior, inferior, and internal, but also the

levator palpebræ that lifts the upper eyelid, as well as the intrinsic muscles of accommodation within the eye itself.

The *trochlear*, or *pathetic* (IV), supplies the superior oblique muscle, which is the most difficult of all the eye muscles to keep working. Thus, there are anatomical and physiological difficulties in maintaining a continuous attitude of piety with upturned eyes.

The *abducens* (VI) actuates the lateral, or external rectus muscle, by means of which the eye is made to sweep the horizon. This is the easiest of all the eyeball movements, and is probably an ancestral, life-saving inheritance, for by its exercise animals can more easily look about and behind themselves, to learn of the approach of their enemies and the presence of their friends.

The abducens further sends a branch to the *retractor bulbi*, a muscle derived from the external rectus, by means of which fishes are enabled to focus the eye. The *nictitating membrane*, or third eyelid of reptiles, birds, and some mammals, is also supplied by the VIth nerve.

E. Trigeminal (V)

The *trigeminal* nerve (V) comes off from the anterolateral region of the medulla in close association with the VIIth and VIIIth cranial nerves, constituting together a most important group for the supply of the head. It has a strong dorsal root and a lesser ventral root. The *Gasserian ganglion* of the dorsal root is the largest of all the ganglia associated with cranial nerves and may be located even outside the cranium in certain vertebrates.

The trigeminal is so called because of its three component branches, the ophthalmic, maxillary, and mandibular.

In fishes the *ophthalmic*, which is sensory in character, joins with the ophthalmic component of the VIIth nerve, and divides into two sub-branches, the *superficialis* and *profundus*, that run to the snout. The former becomes lost in land vertebrates, but the latter remains to supply the eyelid, conjunctiva, tear glands, and mucous membrane of the nasal pit.

The *maxillary* branch is sensory and goes to the teeth of the upper jaw, and the face, while the *mandibular* branch, supplying the muscles of the face and mouth, contains both afferent and efferent neurones, and is consequently mixed in character.

F. Facial (VII)

The VIIth nerve, or *facialis*, arising from the *geniculate ganglion*, undergoes much modification as the result of evolutionary emergence from water to land life, owing to the loss of the lateral line organs and, in higher mammals, to the development of the mimetic musculature of the face.

In fishes and urodeles there are given off three dorsal branches which are suppressed in the Anura and higher vertebrates, namely, the *ophthalmic* to the snout, running parallel with the ophthalmic branch of the Vth nerve; the *buccalis* to the mouth and the middle line of cephalic lateral line organs; and the *external mandibular* to the lower jaw and to the lower line of lateral line organs of the head.

The ventral branch of the VIIth nerve divides into a pre-trematic trunk anterior to, and a post-trematic trunk posterior to the spiracular opening. The pre-trematic trunk is sensory, and consists of a *palatine* branch to the roof of the mouth, and an *internal mandibular* branch (*chorda tympani* of higher forms) to the inside of the lower jaw, and the mucous membrane of the mouth cavity.

The post-trematic trunk is mixed in character, and forms the *hyomandibular* branch, which becomes the *facial* nerve proper, and plays an increasingly important rôle in the development of the muscles of facial expression in man.

The chorda tympani runs between the malleus and the incus bones of the middle-ear cavity in mammals, which, it will be remembered, are transformed skeletal elements from the splanchnocranium of gill-bearing ancestors. This nerve is wanting in birds, where its place is taken by the glossopharyngeal (IX) nerve.

The taste buds on the anterior two-thirds of the tongue in man, and the sublingual and submaxillary salivary glands, as well as the important facial muscles of expression, are supplied by the VIIth nerve.

G. Acoustic (VIII)

The *acoustic* nerve is entirely sensory, with its two ganglia, the *vestibular* and the *spiral* ganglia, embedded in the petrosal bone in animals without a lateral line. When the lateral line is present, the vestibular ganglia are associated with the lateral line elements of the Vth and Xth nerves, constituting an acoustico-lateral system, which has to do with the reception of vibratory stimuli coming

through a liquid, composed either of the water surrounding the lateral line organs, or the endolymph in which the sensory cells of the inner ear are bathed. The lateral line organs are peculiar to water-dwelling vertebrates, such as fishes and amphibians, but the inner ear, which the acoustic nerve supplies, although derived embryologically from the anterior end of the lateral line system, remains constant throughout the vertebrate series.

The VIIIth nerve divides into two branches, the *vestibular* and *cochlear*, which go respectively to the equilibratory apparatus and to the auditory mechanism of the ear.

Proprioceptive stimuli arise from within, which enable the animal to orient itself in space. These stimuli act upon the static apparatus of the semicircular canals, whence they are conducted by the vestibular branch to the brain. *Exteroceptive stimuli* from without, reaching the organism in the form of sound waves, pass to the organ of Corti in the inner ear, whence they are relayed over the cochlear branch to the brain for interpretation.

H. Glossopharyngeal (IX)

The *glossopharyngeal* nerve, with its *petrosal ganglion* that frequently fuses with the ganglion of the Xth, is primarily the nerve of the first gill slit. It has a sensory *dorsal pharyngeal* branch to the lateral line apparatus, and *pre-*, and *post-trematic* branches, extending on either side of the first gill slit, just as the palatine and hyomandibular of the VIIth extend on either side of the spiracle, and the maxillary and mandibular of the Vth, on either side of the mouth.

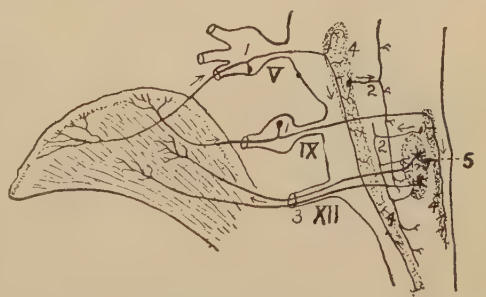


Fig. 605.—Diagram of the tongue and a part of the medulla to illustrate the central connections and functional relationships of certain cranial nerves. *1*, sensory neurones of trigeminal (V) and glossopharyngeal (IX) nerves; *2*, relaying neurones; *3*, motor fibers of hypoglossal (XII) nerve; *4*, sensory nuclei; *5*, motor nucleus. (From Ranson, after Cajal.)

The pre-trematic of the IXth is sensory and goes to the hyoid arch, while the post-trematic is mixed, supplying the pharynx, the taste organs of the tongue, and, in mammals, the tonsils and the epiglottis also.

It is the post-trematic branch of the primitive IXth nerve that eventually becomes the gustatory nerve in higher vertebrates, reaching the taste buds located on the posterior third of the tongue (Fig. 605). It also has efferent components that supply the pharyngeal muscles and the parotid salivary gland.

With the emergence to land life and the suppression of the lateral line, the dorsal-pharyngeal branch, as well as the pre-trematic hyoid branch, lose their significance and disappear.

I. Vagus (X)

The Xth, or *vagus* nerve is apparently a composite of several metameric nerves which have a different development in gill-bearing fishes and amphibians than in land vertebrates. In the former and more primitive group a sensory *lateral trunk*, with its *lateral ganglion*, goes to the lateral line organs, and a second mixed *branchio-intestinal trunk*, with its *jugular ganglion*, extends to the gills and viscera. This latter trunk sends off sensory pre-trematic and mixed post-trematic branches to every gill slit except the first pair, which is supplied by the IXth nerve, and then continues on in close association with the sympathetic nervous apparatus to supply the various visceral organs of digestion, circulation, and respiration.

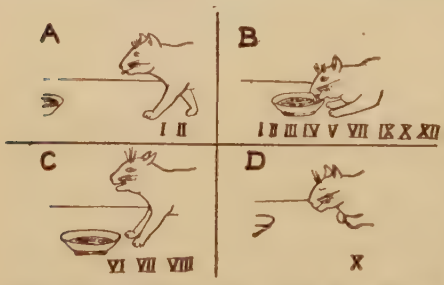


Fig. 606. — The functions of the cranial nerves. *A*, smelling and seeing (I, II); *B*, smelling and seeing (I, II); convergence and accommodation (III); depression of eyeballs (III, IV); mastication (V); salivation and tasting (VII, IX); swallowing, (X, XII); tongue movements (VII). *C*, a moment of vigilance, with outward rolling of the eye (VI); facial and ear movements (VII); listening (VIII); *D*, digesting (X). The only omission is the spinal accessory (XI), supplying certain neck muscles, which may have been used various times in this sequence. (As summarized by Dr. Stanley Cobb, in Stiles' *The Nervous System and its Conservation*. W. B. Saunders Co.)

In amniotes the lateral line trunk, and that part of the branchio-cephalic that goes to the gills, being no longer needed, are for the most part discarded, but a part of the branchio-cephalic branch remains as the large *pneumogastric*, or *vagus nerve*, having afferent and efferent elements and connecting with thoracic and abdominal viscera. It is quite

properly designated as the "vagrant" nerve, since it probably wanders farther than any other, reaching as it does, from the head well into the tail in fishes, and to a distance from its origin relatively as remote in higher vertebrates.

J. Spinal Accessory (XI)

In the lower vertebrates the *spinal accessory*, or the *accessorius Willisii*, as it is sometimes called, is a part of the Xth nerve complex. It becomes established as an independent nerve only in mammals. It is a motor nerve without sensory elements, and supplies the muscles of the shoulder girdle.

K. Hypoglossal (XII)

The *hypoglossal* nerve (XII), like the Xth, was probably made up originally of more than a single pair of nerves. It has lost its sensory fibers and become first included within the cranial group of nerves in reptiles. It is devoted to the muscles of the tongue, and reaches its highest efficiency in man, where the nerve enables him to retract his muscular tongue after it has been extended. It is not so effectual, however, in the more difficult task of retracting anything he may chance to say with his tongue.

The functions of the cranial nerves are cartooned in Fig. 606.

X. THE INVOLUNTARY NERVOUS SYSTEM

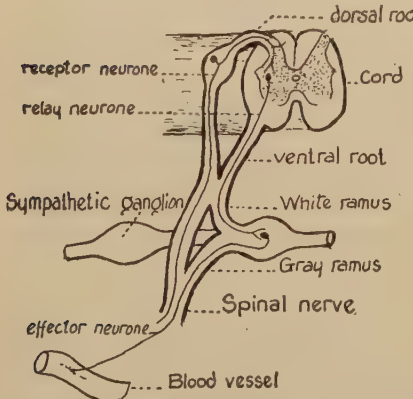


Fig. 607.—Diagram to show the relation of the sympathetic chain to the nerve cord. (After Schimkewitsch.)

Much of the work of the body, particularly of the viscera, glands, circulatory apparatus, and smooth muscles, is regulated by an extension, or understudy, of the nervous system proper, beyond the direct control of the will. This self-regulating mechanism, like that of the voluntary apparatus, is made up of neurones arranged in fibers, ganglia, and plexuses, and is commonly known as the "sympathetic system." By taking over most of the routine drudgery of living, it releases the central nervous system for higher evolutionary adventures (Fig. 607).

It is not, however, a complete system in itself, as is sometimes implied, attending to the involuntary muscles by means of central and radiating parts in the same way that the brain and peripheral nerves attend to the voluntary musculature. It is rather an extension or relay apparatus, consisting of neurones that have either migrated secondarily from the central nervous system, or arisen independently of it, and become peripherally placed in vagrant ganglia and fibers located conveniently near the organs which they

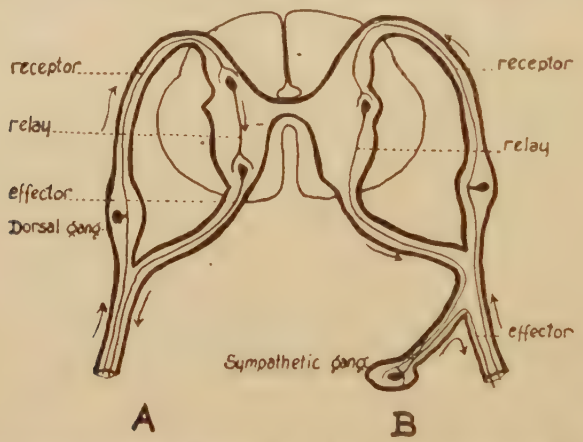


FIG. 608.—Reflex paths in the cord. *A*, of the voluntary system. The receptor neurones run in the dorsal root, their cells lying in the dorsal ganglion. Relay neurones have their cell bodies in the dorsal horn and connect with the effector neurones in the ventral horn. *B*, of the involuntary system. The receptor neurones as in the voluntary system. The relay neurones are drawn down so that their nuclei are in the lateral column region of the gray area, while their fibers form the ventral root and extend to the sympathetic ganglion as the white ramus. The fibers of the effector neurones leave the sympathetic ganglion as the gray ramus, going to make a part of the spinal nerve. (After Gaskell.)

supply, while still retaining their organic dependence upon the main nervous system.

The plan of the neurones of the involuntary apparatus may best be understood by comparing it with that of the voluntary apparatus. Taking the typical arrangement of the neurones of the voluntary system in a spinal nerve, as represented on the left side of Fig. 608, there are seen three nuclear centers, namely, that of (1) the afferent, or sensory neurone in the dorsal ganglion; (2) the efferent, or motor, neurone in the ventral horn of the gray matter within the cord; and (3) the relay neurone, which lies entirely

within the cord, and, with its cell body in the dorsal horn of the gray matter, connects the afferent and efferent neurones. Each of these kinds of representative neurones, many times multiplied in number, together form the voluntary system.

If now, according to Gaskell, the nuclear center of the efferent neurone may be imagined to migrate by way of the ventral root to a new headquarters, or ganglion of its own, quite outside the cord, as shown on the right side of Fig. 608, and at the same time to pull down to a lateral instead of a dorsal position inside the cord the nuclear center of the relay neurone which makes a synapse with it, the essential difference between the involuntary and the voluntary apparatus will be made clear.

It will be seen according to this conception, that the ventral root of the involuntary mechanism is composed of neurites from relay cells whose nucleus is now in the *lateral* horn, while the efferent neurones, which comprize the ventral roots in the voluntary apparatus, no longer emerge from the cord, but pass out through the sympathetic branch from the newly established ganglion, where they join with the relay cells to form a part of the spinal nerve. As a result, the ventral root, so far as the involuntary apparatus is concerned, is not made up of motor neurones, as it is in the voluntary mechanism, but becomes an efferent fiber tract connecting one part of the nervous system with another, just as the optic nerve is not a "sensory nerve" at all, but a *nerve tract*, connecting two parts of the central nervous system. Thus, corresponding to the pairs of craniospinal nerves, a row of central involuntary ganglia is established, which extends from the cranium to the coccyx down either side of the aorta next to the backbone.

There is considerable evidence that the involuntary nervous system should not be regarded as a secondary derivative of the central nervous system, as just indicated, but rather as a primitive ancestral apparatus, more or less homologous with the nervous system of invertebrates, which has become secondarily subservient to the voluntary nervous system in vertebrates. Its cells of origin really arise, as do those of the voluntary peripheral nervous system, from the neural crests which pinch off from the embryonic medullary groove.

According to Kuntz [1] the neurones of sympathetic ganglia arise mainly from the intermedio-lateral position of the gray matter of

[1] *Jour. Comp. Neurol.*, vol. 34, No. 1. 1922.

the cord. This is what one would expect since this region is visceral efferent and is the seat of cell bodies of preganglionic (somatic efferent) neurones which synapse in sympathetic ganglia.

The involuntary ganglia, while retaining their original connection with the central nervous system, become joined together into two longitudinal chains by *interganglionic fibers*, and frequently also by *transverse fibers* that pass from side to side like the rungs of a ladder.

The number of ganglia originally corresponds to the number of craniospinal nerves, but is reduced at birth and no longer has its regular metameric sequence. As a result of this reduction there are in man three pairs of cervical ganglia, ten to twelve pairs of thoracic, four pairs each of lumbar and sacral, and one pair of coccygeal in the involuntary series.

The *preganglionic fibers*, extending from the central nervous system to the ganglia of the involuntary system, are medullated, and form the *white ramus communicantes*. *Postganglionic fibers* of distribution, *rami viscerales*, radiate from the involuntary ganglia to various organs. These are unmedullated and gray in appearance (Fig. 607).

There are present between the central involuntary ganglia and the parts which they supply, still other relaying substations in the form of *collateral* and *terminal* ganglia, as well as numerous *plexuses* of fibers, which facilitate nervous interaction. The largest of these plexuses of the involuntary system is the *solar plexus*, from which radiate fibers to the diaphragm, spleen, liver, kidneys, aorta, heart, pancreas, small intestine, colon, and reproductive organs. A "blow on the solar plexus," therefore, is likely to have as far-reaching results, as the traditional "monkey-wrench thrown into the machinery."

The preganglionic motor fibers between the central nervous system and the auxiliary involuntary system, leave the cord through the ventral roots of the craniospinal nerves by three general outflows (Fig. 609), namely, bulbar, thoracico-lumbar, and sacral, which are separated somewhat from each other by the two voluntary plexuses, brachial and lumbo-sacral, that mark the muscles of the limbs.

The *bulbar outflow* involves parts of the VIIth, IXth, and Xth cranial nerves, and supplies the salivary glands, heart, blood vessels, and small intestine, as well as the bronchi, liver, pancreas, and kidneys. A separate connection occurs also with the oculo-

motor nerve (III) in the cranial region by way of the *ciliary ganglion*, for the involuntary control of the ciliary muscles of the eye and the sphincter muscles of the iris.

The *thoracico-lumbar outflow* goes to the same structures as the bulbar outflow, with the exception of the salivary glands, and, in addition supplies the large intestine, urogenital apparatus, and the involuntary smooth muscles of the skin.

The *sacral outflow* goes to the bladder, genital organs, and to the large intestine and its derivatives.

The efferent fibers of the *white rami communicantes* characterize the thoracico-lumbar outflow, which constitutes the "sympathetic system" proper.

Gaskell puts the bulbar and sacral groups together under the name of the *enteral group* of involuntary nerves in contrast to the thoracico-lumbar, or *sympathetic group*, because of their different behavior when subjected to certain chemical tests. At the time when the neuroblasts migrate out from the thoracico-lumbar region to form the involuntary ganglia, they are accompanied by certain *chromaffine cells* that produce *adrenalin*. This substance eventually becomes centralized in the suprarenal gland as a hormone which has a marked effect upon smooth involuntary muscles. If adrenalin is injected intravenously, the tissues of the sympathetic group, or those supplied by the thoracico-lumbar outflow, will contract, while those of the bulbo-sacral group remain unaffected. On the other hand, when certain chemical substances, such as *acetyl-choline* for example, are employed, the structures supplied by the bulbo-sacral outflow respond, but those of the thoracico-lumbar outflow do not.

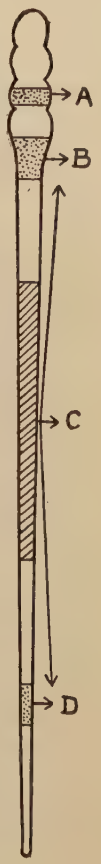


FIG. 609.—Diagram of the central localization of the cerebrospinal visceral nerve connections. *A*, *Mid-brain autonomic* (sphincter of iris and ciliary muscles); *B*, *bulbar autonomic* (heart, blood vessels of mucous membrane of head, salivary glands, walls of digestive tract from mouth to descending colon, including outgrowths of this region, namely, trachea, lungs, gastric glands, liver, pancreas); *C*, *thoracico-lumbar sympathetic* from first thoracic to second and third lumbar, (dilator of iris, orbital muscles, arteries, muscles and glands of the skin, blood vessels of the lungs and abdominal viscera, and of the digestive tract between mouth and rectum, arteries of skeletal muscles, muscles of spleen, ureter, and internal generative organs); *D*, *sacral autonomic* of second and fourth sacral, (arteries of rectum, anus, and external generative organs, walls of bladder and urethra, walls of descending colon to anus). (From Herrick, after Langley.)

The viscera are under nervous control of two sorts, one centering in the ganglia of the involuntary system, and the other in the central nervous system itself. In the latter case, however, the stimulation or inhibition as the case may be, is usually unconscious, and acts *through* the channels of the involuntary apparatus. For instance, the visceral sensory fibers may run straight through the sympathetic ganglia from Pacinian corpuscles in the mesentery, or they may form sensory nerve endings in the mucous membranes, and reach their cell bodies located in the dorsal ganglia of the spinal system. Such fibers are really not an integral part of the involuntary system although incorporated within it.

There is in addition considerable non-nervous control of the viscera through hormones produced by endocrine glands, as when secretin from the intestinal wall, warned by the approach of acidulated food, stimulates the flow of pancreatic fluid from the pancreas.

In amphioxus there is no involuntary nervous system, but in cyclostomes unconnected sympathetic ganglia are established in the body region. Elasmobranchs and perennibranchiate amphibians show an advance, in that a network of fibers connects some of the trunk ganglia with each other. In teleosts a thin trunk line of interganglionic fibers is present, with frequent transverse rami while the Vth, VIIth, IXth, and Xth cranial nerves form a bulbar outflow that extends the involuntary system into the head. In the Anura only the Xth nerve is involved in the extra-sympathetic part of the involuntary system. It is not until the amniotes are reached that the primary involuntary system of the trunk becomes definitely extended to both the cranial and sacral regions. In man, as already pointed out, the original metameric arrangement of the involuntary system is considerably blurred, particularly in the extreme anterior and posterior regions.

Muscular movements produced by the involuntary system of nerve control, are largely generalized, and are by no means as delicately coördinated as in the voluntary nervous system.

CHAPTER XX

COMMUNICATION WITH THE OUTSIDE WORLD (SENSE ORGANS)

I. INTRODUCTION

The sensitive tissues of a living animal are primarily ectodermal in origin and external in position. They do not remain in this exposed situation, however, but become for the most part buried within the protective body, and in this way are shielded from direct impact with the constantly changing outside world.

The withdrawal of the central nervous system from direct external influences necessitates the establishment of peripheral nerves to retain connection with the environment. Since nerve fibers are not so well adapted for reception as for transmission, specialized structures for the purpose of receiving different kinds of stimuli are also required. The latter intermediary structures between the organism and its surroundings, are commonly designated as "sense organs," but it is preferable to call them *receptors*, since not all impressions received through them result in sensation.

It is readily seen that sense organs, or receptors, are an essential part of the nervous system as a whole, being indispensable in acquainting the animal with its food, mates, friends, and enemies, both near and distant, as well as with whatever else goes to make up its particular world.

A *stimulus*, which is something that excites a receptor, bringing about a response of activation or inhibition, is defined by Stiles as "a change, physical or chemical, which is capable of producing physiologic reactions." It may come from the outside in the form of environmental changes of various sorts, or it may arise from processes going on within the organism, as when the production of carbon dioxide in the blood stimulates the respiratory center in the medulla, with the result that the muscles involved in breathing are set into action.

The essential thing about any stimulus is the element of change, or the fact that something different in kind or degree is happening in the surroundings of an animal. As pointed out by Helmholtz, sense organs do not give a true picture of the actual environment in which we live, but only of the changes taking place in it. Long-enduring or constant stimuli, such as balanced odors or the hum of city traffic, become noticeable as stimuli only when they change in intensity.

A wide range of different stimuli may at various times bombard an organism and yet only certain of them have any effect, because of the absence of appropriate receptors, or ports of entry. The persuasive human voice, for instance, means nothing to a deaf goldfish, nor the sudden glare of the sun to a blind mole.

Receptors are generally cells or organs that are specialized to take in impressions of a single kind and no others (Müller's Law). Such receptors are said to be "adequate" for the stimulus in question. The eye is adequate for light, but taste organs only for the chemical stimulation of dissolved substances.

A further advantage of adequate receptors lies in the fact that, by exclusive adaptation to only one type of stimulation, protection may be acquired against the unnecessary annoyance arising from stimuli other than the one to which the receptor has become adapted. The sensory elements of eyes and ears, for example, while retaining a clear pathway of exposure to the stimuli of light and sound respectively, are protected from chemical and contact stimulation, and also from temperature changes; while smell and taste organs, although in a situation convenient to be affected by gases and liquids, are not particularly exposed to mechanical contacts, or the impact of waves of sound or light. It is possible, by becoming oblivious to extraneous happenings, for receptors to gain a high degree of efficiency through specialization.

A special sense organ is one whose *threshold of stimulation* is lowered for one particular type of stimulus and raised for all other types. The particular stimulus to which it is most sensitive is called its *adequate stimulus.*

Sometimes a receptor is acted upon by a stimulus to which it is not adequate. Thus, if the chemical substance menthol is rubbed into the skin, a feeling of cold results instead of a chemical response such as smell or taste; or, if a vibrating tuning fork

is placed upon the tip of the tongue, tickling, which is a form of touch, is the result instead of sound. In these instances the thermal sense endings in the skin are *inadequate* to the chemical stimulation produced by menthol, and the tactile buds on the tip of the tongue to the sound waves from the tuning fork. In this way widely different stimuli may, at times, produce the same general sensation. For example, the idea of light may be conveyed not only by a luminous object, like the flame of a candle, or the shining sun emanating light waves, but also by a mechanical blow on the back of the head, making one "see stars," or by simple pressure upon the eyeball of the closed eye.

It must be continually borne in mind that sensation is a function of the central nervous system, and that sense organs, or receptors, are simply avenues of approach. One does not see *with* a pair of spectacles, but *through* them. Much confusion frequently results, particularly in the more obscure types of reception, since it is customary to refer a sensation to its receptor, as when one "feels" a pin prick in the finger tip at the point where contact is made, rather than to the brain, where sensation actually occurs. In the case of amputation, sensations to which the missing parts were formerly subjected are still referred to the latter by the injured person.

When one realizes how easy it is to have sensory illusions of every kind, and how variable the central judgment can be upon the "evidence of the senses," not only in the same individual on different occasions but also on the part of different individuals on the same occasion, it is small wonder that mankind, even with the best of intentions, finds the goal of absolute truth very elusive and always difficult to attain.

Owing to the specialized selectivity of different kinds of receptors for particular stimuli, and the largely variable subjective element that has so much to do with the use made of sense organs, it is extremely doubtful how dependable is the knowledge possessed about the sensory life of animals other than ourselves. Even in the case of other human beings, with a sensory equipment apparently quite like our own, we can only infer what the sensations experienced are like. It is necessary with regard to animals, having receptors and a central apparatus unlike that of man, to resort solely to observation of behavior resulting from the application of some particular stimulus in order to make

any reasonable guess as to how the animal feels under the circumstances. Behavior, moreover, is not in all cases a safe criterion on which to depend, for a responding animal does not always do what we would do, or some other animal might do, under the same conditions. Similar movements, therefore, do not necessarily express similar feelings, for when a friendly dog wags its tail, it portrays an entirely different state of mind from that of an excited cat, lashing its tail back and forth. It is particularly embarrassing for man, whose tail is only an evolutionary memory, to try to pass active subjective judgment on the feelings that find expression in tail movement. Naturally the more unlike man an animal is, the more uncertain must be the human interpretation of the world in which it lives.

Receptors in an animal may be structurally quite different from those in man, admitting stimuli entirely outside the range of human possibilities, or excluding those for which man has an adequate sensory equipment. In other words, every animal lives in its own changing world of stimuli to which it has become more or less accustomed, while its responses within that world are determined by the particular nervous organization with which it is endowed, and by the gamut of its receptive capacity. Thus, the range of vibrations which stimulate the human ear as sound, lie between approximately 16 per second and 41,000, while the range of the visible spectrum is between 481 billion ether waves per second at the red end, and 764 billion at the violet end. Outside of these extremes, human sense organs receive neither sound vibrations nor light waves, and under such conditions neither hear nor see.

The receptive range of other animals is unlike that of man and may extend even beyond it. Cats, for example, are known to respond to higher tones than are perceptible to human ears; ants, subjected to a field in which the light is broken up into the components of the spectrum by a prism, arrange their pupæ with reference to ultraviolet light that is unseen by the human eye; dogs perceive odors of which man knows nothing; and houseflies distinguish the difference between sugar and saccharin which to the human tongue taste alike.

The interpretation of the stimuli admitted through the receptors always depends upon the brain, or "the man behind the gun." Birds upon a battlefield are apparently not alarmed by the terrible

crash of exploding cannon, continuing to sing and fly about as usual; while the picture of a mouse, however well done, awakens no interest when placed before the eyes of a hungry cat.

In structure all receptors consist of essential sensory units, or cells of ectodermal origin. These may be accompanied by accessory cells or tissues of either ectodermal or mesodermal derivation, that are responsible for most of the elaborate differences which characterize various sense organs. As would be expected, the least morphological complication is found in receptors of the more primitive aquatic animals. The transition to land life, with consequent access to a wider range of stimuli, has been invariably accompanied by an increased differentiation in the structure of the receptor organs. Nevertheless, in the highest land vertebrates, the essential sensory cells of such an elaborately specialized sense organ as the ear, are still bathed in fluid, as are the more primitive receptors of aquatic forms.

In nearly all cases, the sensory receptors of vertebrates are protected from mechanical injury. Eyes are housed in sunken skeletal orbits in the skull; the sensory parts of ears are embedded entirely within cartilage or bone of the cranial wall; the olfactory epithelium is safely concealed upon the inner wall of the cavernous nasal pits; the organs of taste are inside the mouth cavity behind closing jaws; and even the sense organs of temperature, pain, pressure, and touch, which are located in the exposed skin, are in many instances either sunken below the surface, or surrounded by an individual barricade of non-sensitive, protective cellular material.

II. THE CLASSIFICATION OF RECEPTORS

The old subjective classification of the senses into touch, smell, taste, sight, and hearing, is no longer sufficiently inclusive, for there are nearer twenty-five than five different kinds of receptors that can be distinguished in man alone, not to mention additional ones which characterize animals other than man.

By considering the adequate stimulus of receptors, rather than the sensations produced through them, an objective instead of a subjective basis is gained for classification of receptors, making possible not only more accurate description, but also the inclusion of certain known receptors for which no corresponding sensation is recognized.

Classifying the receptors first in accordance with the source of

the stimulus, there are three great groups, designated by Sherrington as *exteroceptors* or those whose stimuli come from the outside, and *interoceptors, and proprioceptors*, with stimuli arising within the organism itself. Exteroceptors receive mechanical, chemical, and radiant stimuli from the outside, while the more deeply-seated interoceptors, associated primarily with the digestive tract, respond to stimuli of hormonic, formative, trophic, noxic, and catabolic nature. Proprioceptors have to do with the control of the musculature as a whole.

The following table gives this arrangement of stimuli, together with the corresponding sensations produced, and the receptors involved.

TABLE OF CLASSIFICATION OF STIMULI AND RECEPTORS

I. Outside sources	*Exteroceptors*	
1. Mechanical stimuli		
A. Temporary contact	Tangoreceptors	Touch
B. Vibratory contact	Phonoreceptors	Hearing
C. Intensive contact	Algesireceptors	Pain
D. Currents of water	Rheoreceptors	Orientation
2. Chemical stimuli		
A. Gases	Olfactoreceptors	Smell
B. Liquid solutions	Gustoreceptors	Taste
C. Irritable substances	Irritoreceptors	Irritation
3. Radiant stimuli		
A. Thermal	Caloreceptors	Heat
B. Thermal	Frigidoreceptors	Cold
C. Photic	Photoreceptors	Sight
II. Inside sources		
1. Alimentary control	*Interoceptors*	
2. Muscular control	*Proprioceptors*	

For purposes of description, receptors may be grouped into (1) cutaneous sense organs; (2) special chemical senses; (3) the master senses of hearing and sight; and (4) internal sensory mechanisms.

III. CUTANEOUS SENSE ORGANS

The sense organs of the vertebrate skin include a considerable variety, among which are organs of touch or pressure, temperature, pain, and in some aquatic forms, taste, and lateral line organs that are stimulated by currents of water. Some of these cutaneous organs are also distributed in the mucous membranes that line passage-ways into the body, particularly in the transitional region between the exposed skin on the outside and the

moist mucous lining within. There is an evolutionary tendency for sensory receptors to withdraw from their original position directly at the surface of the skin. This is particularly true in land forms, whose skin is exposed to dry air, thus necessitating ecdysis or the periodic removal of the dead outer corneal layer. It is an obvious advantage when ecdysis does not involve sense organs located in the skin, since specialized neurones are not adapted, as are less elaborated cells, to renewal by mitosis. In most aquatic vertebrates where there is not a great need of ecdysis, the primary superficial location of the sensory neurones is common, but among vertebrates amphioxus is the only representative having true single peripheral cutaneous sensory receptors.

In other vertebrates the sense organs of the skin are secondary in location, that is, withdrawn from the surface. The sensory cells of the olfactory epithelium form an apparent exception, but they do not properly belong in the group of cutaneous sense organs.

Fig. 610.—Nerve endings around the base of a hair of a white mouse. (After Szymonowicz.)

Upon assuming a deeper position, secondary sensory neurones extend their receptive dendritic processes toward the surface and the source of stimulation. These processes may either end freely between the cells of the skin, or they may terminate in intimate relation with some sort of an accessory apparatus which acts as a *stimulator*, or non-nervous, mechanical intermediary between the receptor itself and the stimulus. The stiff "whiskers" (vibrissæ) of a cat, for example, transfer the stimulus of mechanical contact to deep receptor neurones, whose dendrites form a brush or a net around the embedded ends of the vibrissæ (Fig. 610).

1. Tangoreceptors

All receptors which transfer mechanical disturbances of gases, liquids or solids, that are in direct contact with the body, are classified as organs of touch, but when touch is sustained beyond transient contact, they are interpreted as organs of pressure.

The contact sense is the most universal and unavoidable of all the means of communication between an organism and its environment. It is possible to close the eyes and ears against sights and sounds, or to avoid the chemical stimuli that lead to taste and smell, but it is not easy for a body of three dimensions to escape

from contact with objects that surround it. Touch is also the great confirmatory sense, bearing supplementary witness particularly to the sense of sight. A baby, for example, never discovers its toes by simply gazing at them, for it is only when it accidentally grasps them in its exploring fingers that it joyfully recognizes them as its own.

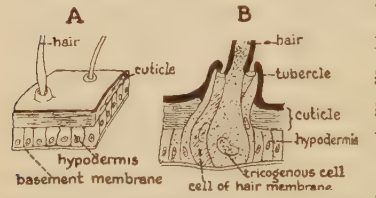


FIG. 611.—Diagrammatic representation of a portion of the body-wall of a bee, bearing a corneal or tuberculate "hair." *A*, a piece of the body-wall, bearing two "hairs;" *B*, section through the base of a "hair." (After Snodgrass.)

While widely scattered, tango-receptors are not universally distributed throughout the skin, but are placed in locations where they are most likely to come into contact with external objects. Thus, in man the knee is more sensitive to touch or pressure than the thigh, and the friction areas on the inside of the hands or feet, than the scalp. The concave surface of the curving tail of the spider monkey, *Ateles* (Fig. 199), is bare of hairs and richly supplied with organs of touch, because this animal makes constant tactile use of the tail in its arboreal adventures. In fact there seems to be a reciprocal relation between the presence of hair in the mammalian skin, and specific tactile organs, just as in birds the organs of touch are confined mostly to those parts that are devoid of feathers.

FIG. 612.—An end bulb of Krause. The same general structure is seen as in the Vater-Pacinian corpuscles (see Fig. 614), but this sense-organ is better adapted to its position between muscle fibers. (After Dearborn.)

Scaly reptiles, in addition to the development of a highly tactile tongue, have either corneal "hairs" similar to the "hairs" on a bee (Fig. 611), that act mechanically upon sensory receptors embedded in the skin below, and which are shed at ecdysis with the scales upon which they grow, or certain of the scales may be penetrated by small pores, through which cutaneous tangoreceptors gain access to outside contacts.

Not much is known about the organs of touch in the skin of fishes and amphibians. Certain sensory *terminal buds* have been demonstrated in the connective tissue at the base of the fins in elasmobranchs, and there is little doubt that the barbules that dangle around the mouth of such bottom-

feeding fishes as the catfish, *Amiurus*, act as "feelers." In amphibians the mucous membrane covering the tongue is surely sensitive to touch, as well as that of the flickering protrusible tongues of snakes, but specialized tangoreceptors in the skin, separate from free nerve endings, have not been definitely demonstrated in these animals.

It is in the mammals that the tangoreceptors reach their greatest elaboration and have been most studied.

In addition to the tactile nerve endings, which terminate freely between the cells of the skin, there may occur modifications whereby the dendrites of sensory neurones are enclosed in capsules of varying complexity, thus increasing the effective surface which is exposed to contact. Such are the *Krause end bulbs* in the mucous

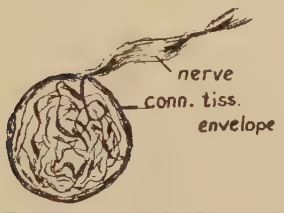


FIG. 613.—A Golgi-Mazzoni corpuscle, from the edge of the conjunctiva in man. (After Wiedersheim.)

FIG. 614.—A Vater-Pacinian corpuscle. (After Plate.)

FIG. 615.—Merkel's tactile cells, from the snout of a pig. (After Tretjakoff.)

membranes of mammalian lips, tongue, mammary glands, and conjunctiva (Fig. 612); the *Golgi-Mazzoni end bulbs* in the corium of the finger tips and external genitalia of man, and in the snouts of cattle (Fig. 613); and the *Vater-Pacinian corpuscles* in the subcutaneous layer of the skin, as well as even deeper in tendons and joints, in the pleural walls, around the larger blood vessels, and in the peritoneum and mesentery of the body cavity (Fig. 614).

Of the types of tangoreceptors that make use of accessory nonnervous cells, the simplest are *Merkel's corpuscles* (Fig. 615), in which the end of the dendrite forms a cup fitting under an epithelial cell that acts as a stimulator. Whenever such an epithelial cell is agitated by contact, the stimulus is received by the enfolding tip of the tangoreceptor cell, and transferred to the brain, with the resultant sense of touch or pressure. In this case the nonnervous stimulator cell is larger and more likely to effect a contact

with something outside than a slender free intercellular nerve ending would be.

Another similar mechanism, *Grandry's corpuscles* (Fig. 616), which is found only in the mouth parts of birds, consists of two large disclike stimulator cells with nerve endings from a sensory neurone sandwiched in between them, the whole packet being surrounded by an envelope of connective tissue. The so-called *Herbst corpuscles* (Fig. 617), likewise found only in birds, consist of two rows of stimulator cells arranged along a neural core within a capsule. They are distributed within the mouth parts, between certain muscles, and in the areas of skin that are comparatively free from feathers.

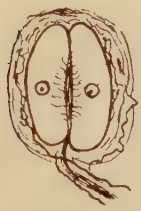


Fig. 616.—Grandry's corpuscle, consisting of two sensibilator cells with nerve endings between them. (After Dogiel.)

Finally, *Meissner's corpuscles* (Fig. 618), which occur only in the friction areas of the skin of primates, resemble highly elaborated Grandry's corpuscles, but instead of two, there is an irregular pyramid of stimulator cells, interlacing with the branching ends of dendrites from sensory neurones in the corium, the entire mass enclosed in a capsular sheath. These are the sense buds that form the sensory papillæ just below the epidermis along the friction ridges on the finger tips (Fig. 124), and which make the fingers such delicate and effective organs of touch.

Fig. 617. — Herbst's corpuscle from tongue of a duck. (After Plate.)

Fig. 618.—Meissner's tactile corpuscle (stained with gold chloride), within a papilla of the skin of the hand. (After Ranvier.)

While tangoreceptors are usually concerned only with actual contact, there is some evidence that they aid, possibly through pressure resulting from intervening air currents, in determining the presence of near-by objects. A blind person, for example, whose tactile senses have become compensatingly sharpened, is frequently aware of the neighborhood of a wall which he may be approaching, before he comes into direct contact with it.

Spallanzani (1729–1799) long ago discovered that a bat was still able to avoid a maze of strings stretched across a chamber, even after it had become blinded. The result of this classic experiment is not to be so much wondered at when it is remembered not only that bats are naturally active at twilight, a time when dependence upon sight in avoiding obstacles and encountering insect prey is of much lessened importance, but also that there are many thousands of sensory hairs over the surface of the membranous wings, marking the presence of special tangoreceptors, and that the large upstanding external ears of these flying mammals (Fig. 619) are abundantly supplied with sense organs of touch and pressure.

Fig. 619. — Sensory ear of a bat, *Emballonura*. (After Flower.)

2. Thermoreceptors

Every animal or plant has an optimum range of temperature in which it can most successfully carry on its activities and upon which its distribution over the earth very largely depends. Whenever the temperature departs from this optimum the organism becomes increasingly handicapped, and finally extremes may be reached under which life is no longer possible. The range of temperature in which organisms can continue active, is somewhat less than that in which they can remain alive. Thus, hibernating animals recover from the torpor produced by extreme cold, and likewise from the rigor of inactivity resulting from extreme heat, if the latter is not too prolonged or excessive.

The cause of death is not the same at the two extremes of temperature. An *Ameba*, for instance, when subjected to increasing temperatures, at first becomes more active and then later entirely withdraws its extended pseudopods until it exposes the least possible surface, finally dying from coagulation of the protoplasm. If the temperature is gradually lowered from the optimum, the pseudopods remain extended but movements become more and more sluggish until, in the end, the animal freezes in an expanded condition. Organisms that contain very little water, like seeds and highly desiccated animals, can withstand very low temperatures. It is even possible for certain species, probably as the result of continued selection, to exist under extremes of temperature which are ordinarily fatal, as, for example, in hot springs and in solid

ice. "Thus the effect of high temperatures is principally chemical, involving the living plasma; that of low temperatures is principally mechanical, involving the water of the body" (Davenport).

Changes in temperature act as stimuli to organisms, by means of which their behavior is largely regulated.

Forelle observed that frogs, which ordinarily swim at the surface of the water, take to the bottom when the temperature drops to about 50° Fahr., and Dolbear discovered that tree crickets at 60° Fahr., were found to chirp ninety times per minute, varying four chirps for every degree of deviation from that standard. At 55° the number of chirps is 71, and at 75°, 150 chirps per minute, showing that these vociferous animals are so absolutely dependent upon the exact degree of temperature in which they find themselves, that they constitute an audible thermometer of considerable accuracy.

Thermoreceptors are in most cases free nerve endings, confined to the skin, being absent in the viscera. They are of two types, namely, *caloreceptors* and *frigidoreceptors*, which transmit the sensations of warmth and cold respectively. The former lie deeper in the skin and are less numerous than the latter.

The caloreceptors upon the cheeks and forehead are highly sensitive, as are also those of the palms of the hands, which one naturally spreads out before the fire upon a cold day. They, as well as frigidoreceptors and tangoreceptors, are absent from the front face of the eyeball, although receptors for pain are abundant there. As a matter of fact, caloreceptors are frequently confused with *algesireceptors*, that is, receptors for pain, while frigidoreceptors and sense organs of touch are apt to be associated together. Cocaine, applied to the skin, temporarily destroys the effectiveness of tangoreceptors and algesireceptors, but leaves thermoreceptors unaffected.

Owing to their nearness to each other and the irregular way in which they are intermingled, accurate discrimination in the sensations produced by the stimulation of dermal sense organs generally, is very difficult. In the case of thermoreceptors the resulting response is particularly conditioned by the *number* of receptors involved. The total effect experienced when an exploratory foot is plunged into a cold bath is quite different than when the whole body is submerged at once.

Confusion may also arise with respect to the stimuli which affect the temperature senses, since stimuli coming from outside sources, and internal ones resulting from the previous condition within the body, both play a part in determining the resultant feeling. If one hand is immersed for a few moments in ice water at the same time that the other is thrust into hot water, and then both are withdrawn and plunged together into tepid water, the former hand will "feel" warm and the latter cold, although both are being subjected to the same thermal stimulus.

Goldschneider, with meticulous exactness, located upon his own skin, warm and cold spots over small areas (Fig. 620) and then with commendable scientific zeal, cut out pieces of this charted skin, which, after sectioning and staining, he subjected to careful microscopic examination. He found nerve terminals that corresponded to the warm and cold spots, and drew the conclusion that these were the real thermoreceptors.

Fig. 620. — Outlines of heat spots and cold spots. Heat spots are cross hatched and dark; cold spots are dotted and light. There is a slight overlapping in a few places. (After Goldschneider.)

Little is known of thermoreceptors aside from free nerve endings, particularly in vertebrates other than man. In the cornea and conjunctiva of the eye, which are sensitive to cold but not to heat, numerous Golgi-Mazzoni corpuscles are found. These may be frigidoreceptors or algesireceptors instead of tangoreceptors, for, since the slightest contact in these parts, such as that caused by a cinder in the eye, results immediately in pain, it is unlikely that organs of touch are present.

That thermoreceptors are distinct from other cutaneous sense organs is well established since they not only have a differential distribution, but also behave differently upon being subjected to anesthesia. Following transplantation operations, too, the invasion of the newly formed skin by different receptors is not simultaneous, the sense of touch being first reëstablished, followed by pain, and finally by the temperature sense.

3. Algesireceptors

Pain is felt through specialized nerve endings, termed *algesireceptors.* Painful sensations, which may result from excessive stimulation of other sense organs, are not to be confused with the special pain arising through algesireceptors. Thus, a piercing tone, too brilliant light, immersion in ice water or scalding water, or strongly applied pressure, may each result in an unpleasant sensation through sensory channels already established for other uses. "The constantly smouldering embers of sensibility," says Foster, "may at any moment be fanned into the flame of pain." Nevertheless, the fact that pain may be experienced in the absence of specific sense organs adequate for other stimuli, for example, as when pain but not touch, is recognized in locomotor ataxia, indicates the separate existence of true algesireceptors. Sometimes a part, while retaining a high degree of touch or pressure sense, is comparatively non-sensitive to pain, as, for example, the inner wall of the cheek. It is not always easy to localize pain at the exact point of origin. Thus, a toothache seems to involve the entire jaw, and a cinder the whole eyeball, while lame chest muscles are often described as sore lungs.

Messages of pain usually demand immediate attention, since they indicate that something is wrong. In this sense Sherrington's term of *nocireceptors,* or receptors concerned with *injuries,* is particularly appropriate. It is far more important to be warned of injury in time by nocireceptors, than to be regaled with delights, optical, auditory, tactile, or chemical, as the case may be, that constantly assail the other sense organs, and which rarely if ever admit stimuli fatal to life. Algesireceptors, therefore, play a peculiarly important rôle in the well-being of the individual, and are in consequence very numerous and widespread, not only over the skin, but also in the underlying organs.

It has been estimated from careful mapping of certain cutaneous areas, that in the entire skin of a normal human adult there are present 30,000 caloreceptors; 250,000 frigidoreceptors; 500,000 tangoreceptors; and 4,000,000 algesireceptors. This ratio of approximately 2:13:25:200, indicates how far algesireceptors outnumber all the others.

Such an enormous equipment for the detection of pain is far more elaborate in man than in other animals, and varies greatly within the human species. Fortunately many injuries, like wounds, do not result in pain in proportion to their extent. For instance, in the amputation of a leg or arm the chief pain comes largely from cutting through the sensitive skin.

There are no specific centers in the brain for the response of pain, such as are known to exist for the senses of sight, hearing, smell, and taste.

4. Rheoreceptors

Certain cutaneous sense organs, arranged around the head and down the sides of the body of fishes and aquatic amphibians (Fig. 621), are termed *rheoreceptors*, or current receptors, which probably aid in orientation with reference to flowing water.

Fig. 621.—Arrangement of the rheoreceptors over the skin of the blind cave "olm" of Germany, *Proteus*. *D*, dorsal; *L*, lateral; *V*, ventral line on trunk. (From Hesse, after Malbranc.)

These structures are connected with cranial, rather than spinal nerves, as are other cutaneous sense organs, and consist of groups of sensory neurones, each provided with a delicate excitatory hair, and enclosed by a barricade of non-nervous supporting cells (Fig. 622). The hairs project into the surrounding water, or, when a cluster of sensory cells becomes sunken somewhat below the surface of the skin, like the crater of a miniature volcano, the pit which is formed is filled with mucus, thus enveloping the hairs and serving as a medium of communication through which the stimulus received must pass, on its way to the receptor cells.

Fig. 622.—Section through a sense organ of the lateral line of a newt, *Triturus*. (After Kingsbury.)

Sense organs of this sort are entirely absent in land vertebrates, but four general kinds have been recognized in fishes and aquatic amphibians, as follows: (1) scattered pit-organs; (2) lateral line organs; (3) ampullæ of Lorenzini; and (4) vesicles of Savi.

Scattered *pit-organs* are independent groups of receptor cells,

distributed mostly over the head, which may be isolated from each other or arranged with considerable regularity either in rows at the bottom of curving grooves, or in sewer-like canals that open by pores to the outside (Fig. 623). The most constant of these alignments, as seen on the head of an elasmobranch fish (Fig. 624), are the *supraorbital* above the eye; the *suborbital*, below the eye, the *infraorbital*, along the ventral side of the snout; the *mandibular*, to the lower jaw; the *hyomandibular*, to the region of the spiracle; and the *supratemporal*, over the top of the head connecting the systems of the two sides.

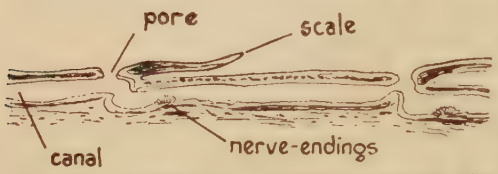


FIG. 623. — Diagram of a section through the lateral line of a fish, *Gobio*, showing pores; lateral line canal; and sensory receptors. (After Leydig.)

The lateral line organs are arranged primarily in three parallel rows down each side of the body. In most fishes only the middle row remains, and this is supplied by the lateral branch of the vagus (Xth) nerve, running along the line of demarcation between the dorsal and the ventral musculature of the trunk. The openings of the lateral line organs in fishes are either between the scales (Fig. 623), or through pores penetrating the scales.

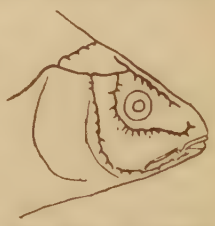


FIG. 624.—The chief canals of the pit-organs on the head of a carp. (After Merkel.)

Whenever lateral fins are so placed that they would naturally extend over a portion of the lateral line, or by their movement cause an agitation in the water which would interfere with the reception of the stimulus produced by external currents of water, that part of the lateral line involved, may curve out of the way to avoid this interference (Fig. 625).

Various stages of elaboration may occur at the same time in different regions of the same fish, or at different times during the course of its development. The eel, *Anguilla*, for example, during the early "leptocephalus stage," has only isolated pit-organs present on the head region, young fingerlings develop a lateral line closed anteriorly but open posteriorly, while the adult has the entire system insunken and closed except for crater-like pores along the line.

Among amphibians rheoreceptors are always present in larval and perennibranchiate forms, the lateral line being usually represented by three parallel rows of isolated clusters (Fig. 621). Traces of these structures remain in some land amphibians in the form of unpigmented spots on the skin, indicating the locality of sensory clusters which have probably become tactile in function.

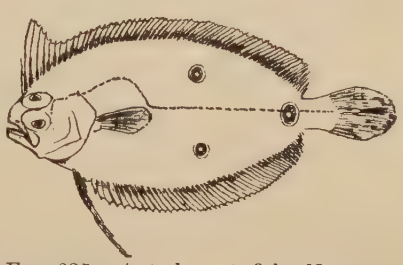


Fig. 625.—A teleost fish, *Notosema*, showing a kink in the lateral line, which thus may avoid currents produced in the water by movements of the pectoral fin. (After Goode and Bean.)

The *ampullæ of Lorenzini*, as well as the *vesicles of Savi*, are highly modified pit-organs, which occur only in elasmobranch fishes. They are deeply sunken below the surface, the former enlarging to a bulblike cavity at the bottom of an elongated duct (Fig. 626), and the latter becoming entirely closed off from the outside. Both are equipped at bottom with receptor cells, surrounded by abundant mucus, and terminating with sensory hairs. The *vesicles of Savi* are found only in the aberrant electric fish, *Torpedo*, where they lie along the outer edge of the electric organ on either side, and around the border of the nasal pits. They are supplied by a branch of the Vth nerve, but their function is unknown.

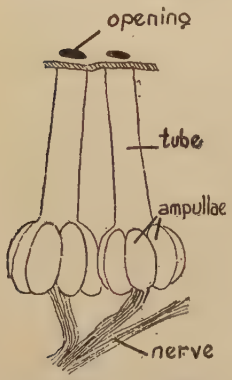


Fig. 626.—Two *organs of Lorenzini*, from a dogfish, *Scyllium*. (After Haller.)

The presence of mucus in the lateral line system and the related structures generally, led at first to the idea that these organs were glandular and primarily secretory in function, but the discovery by Leydig in 1850 that they have a sensory, rather than a motor nerve supply, placed them definitely in the category of sense organs. Subsequent experimentation on fishes, by cutting different nerve supplies, showed that these sense organs make the animal receptive to coarse vibrations traveling through the surrounding medium, as well as to the impact of water flowing in the form of currents. By means of these organs a fish is enabled to face against the current, even in dark-

ness or in turbid waters when "landmarks" are not visible, and so to maintain its position without being constantly carried downstream, or away with flowing tides and currents. Rheoreceptors no doubt also help in making a fish aware of the approach of enemies, who agitate the water in swimming, producing a current of low vibrations which acts as a warning stimulus.

5. Irritoreceptors

The moist skin of amphibians and fishes is sensitive to certain chemical solutions that act as irritants. In reptiles, birds, and mammals, whose integument is adapted to the conditions present in dry air, the stimulus produced by common chemical irritation aside from that interpreted as taste and smell, is confined mostly to moist mucous surfaces. Here it may be very noticeable, as when ammonia causes "watering" of the eyes, or, if inhaled across the mucous surfaces of the respiratory passages, brings about choking reflexes.

The cutaneous sense organs of chemical irritability are closely related to those of contact and pain, but are, nevertheless, distinct from them, as is demonstrated by the fact that cocaine differentiates them from each other, and also because they do not become simultaneously exhausted upon rapidly repeated stimulation. Parker has shown that the tail of amphioxus, for instance, after it no longer responds to the application of weak nitric acid, is still fully sensitive to the touch of a camel's-hair brush. Cole, on the other hand, has demonstrated that a frog, anæsthetized by a 1 per cent solution of cocaine to the point that it is entirely oblivious to the mechanical stimulation of pinching or scratching, will still respond vigorously to the application of a salt solution. "We are, therefore, entirely justified," says Parker, "in concluding that the common chemical sense is a true sense with an important set of receptors and a sensation quality entirely its own."

By experiments of elimination it has been shown that irritoreceptors are free nerve endings with spinal or cranial connection, whose distribution is confined to the skin of aquatic vertebrates or to the moist cutaneous surfaces of land forms.

IV. SPECIAL CHEMICAL SENSES

The chemical stimulation of taste and smell is brought about by contact with solutions of various substances. Liquids are tasted

and gases are smelled. In order to taste a solid object it must first be reduced to liquid form, and even gases must probably be dissolved in liquid before they can be smelled, since the delicate terminal hairs of olfactory receptors are effective only when surrounded by mucus or water in which the odoriferous gases may be received.

Both of the special chemical senses of tasting and smelling are primarily located, like Bunyan's lions before the gates of the Palace Beautiful, near the entrance of the digestive tract, where they may pass upon the character of the entering food. Tasting is necessarily always a matter of direct contact, but smelling, which makes an animal also aware of odorous substances, even at some distance, has the wider range of the two senses, for it serves not only as a food censor, but also directs locomotion in the quest for food and localizes the presence of enemies. It plays an important rôle too in sexual allurement, particularly among mammals, whose glandular skin produces many characteristic odors.

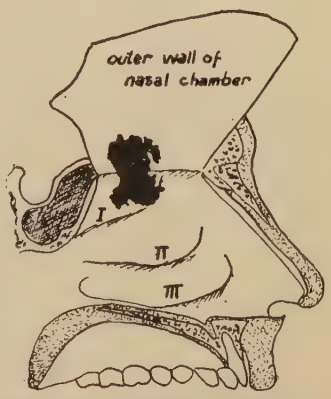


Fig. 627.—Diagram showing the extent and position of the *Schneiderian membrane* (black) in man. The outer wall of the nasal cavity is represented as cut loose along its lower margin and swung upward. *I*, *II*, *III*, conchæ. (From Hesse, after von Brunn.)

1. Olfactoreceptors

Since smell, as contrasted with taste, has a much wider functional range, there is a greater elaboration of accessory structures in the olfactory apparatus than is necessary with organs of taste. There are not only (a) the olfactory neurones themselves, but also (b) the skeletal capsules and cavities in which they are housed; (c) various supplementary chambers, or sinuses, connecting with the olfactory cavities; (d) different devices for securing the passage of odorous substances across an adequate surface of receptors; and (e) glands for maintaining a constant film of moisture over the delicate olfactoreceptors.

A. Olfactory Epithelium

The cellular units of the olfactory epithelium, or *Schneiderian membrane* (Fig. 627), as it is called, are of three kinds, sustentac-

ular, basal, and sensory, of which the latter are the olfactoreceptors. They are unique among vertebrate receptors in that they are of the primitive ganglionic bipolar type, and are peripherally placed, with no synapse such as occurs in other vertebrate sense receptors between the receptor cell and the afferent neurone that connects with the brain. Thus, the neurite of the olfactoreceptor itself forms the olfactory "nerve," which reaches the olfactory lobe, or central nervous apparatus, directly. As this arrangement is not unusual in invertebrate animals, vertebrate olfactory receptors

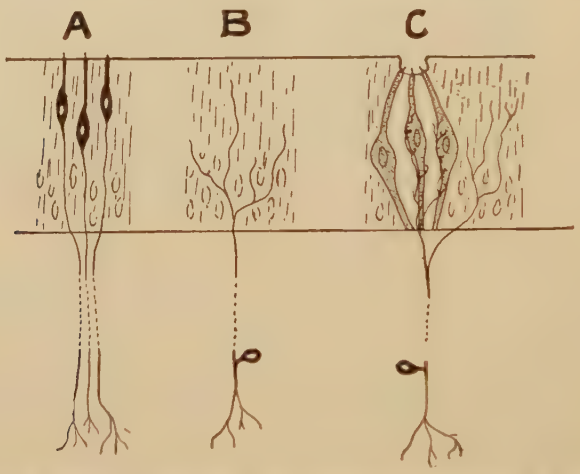


FIG. 628.—*A*, primary sense cell from olfactory membrane; *B*, free nerve endings; *C*, secondary sense cells (taste cells). In the two latter cases the nuclei of the receptors are withdrawn from the surface.

may in a way be regarded as having been rather directly derived from invertebrate ancestors, a supposition not so obvious in the case of other special sense organs, as, for example, the eye and ear.

At the exposed elongated ends of the olfactoreceptors is developed a cluster of extremely delicate protoplasmic processes, or cilia, which may be seen after careful staining with osmic acid (Fig. 628, A). These constitute the most receptive part of the receptor cells, and are protected from injury by mucus produced from the surrounding cells, which also serves as a medium for dissolving stimulating odorous gases.

B. The Nasal Cavities

The olfactory apparatus is the most anterior of all the sense organs. In man it appears first in time at about the third week of fetal existence, as a pair of ectodermal patches on the antero-lateral region of the head. A week later the cells of these patches, which are destined to form the olfactory epithelium, have become depressed into two nasal pits in close approximation to the olfactory lobes of the brain. These pits are brought into communication with the mouth cavity by a channel, the *naso-labial groove* (Fig. 629), extending from the edge of each pit to the mouth, forming a passage-way that eventually becomes closed off and enlarged into the nasal cavities, which are, therefore, in reality an integumental invagination, or part of the outside body which has come to occupy an inside place. Failure of the proper closure of the naso-labial groove, results in the deformity known as "hare lip" (Fig. 630).

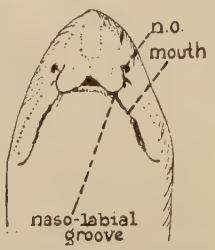


Fig. 629. — Ventral view of the head of a shark, *Scyllium*, showing the naso-labial groove. *n.o.*, nasal opening. (After Schimkewitsch.)

The enlarged nasal cavity finally becomes differentiated into three regions, (1) vestibular; (2) respiratory; and (3) olfactory. They are distinguishable from each other by the character of the epithelium which lines them.

The *vestibular region* is transitional between the skin on the outside and the mucous membrane within. Characterized by the presence of sebaceous glands in mammals, and by outward-projecting, dust-arresting hairs, it forms that part of the nasal cavity which is principally under the protection of the projecting cartilaginous elements of the external nose, when such a structure is present.

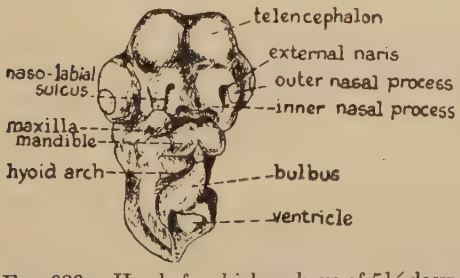


Fig. 630.—Head of a chick embryo of 5½ days, showing the naso-labial sulcus, which would form a "hare lip" if it remained unclosed. (After Duval.)

The *respiratory region* of the nasal chamber is the most extensive part of all. It is lined with ciliated epithelium, and provides space

for the passage of air to and from the lungs. Its walls are very vascular and richly supplied with mucous glands, thus serving to warm and moisten the respiratory current as it enters.

Finally, the *olfactory region* is the innermost recess on either side of the nasal cavity. In man it is comparatively small, the Schneiderian membrane lining it occupying a total area of only about six or seven square centimeters.

The development of the nasal cavities in man finds a parallel in the evolution of these structures in the vertebrate series.

Fishes generally have olfactory pits that are *cul-de-sacs*, not extending into the mouth cavity. The nasal pits of elasmobranchs, however, are on the ventral side of the snout not far from the mouth, and connect with it by means of open naso-labial grooves (Fig. 629). In the Dipnoi, and more completely in the Amphibia, the grooves become closed, thus establishing, in addition to the *external nares*, or nasal opening, a pair of *internal nares*, or *choanæ* (Fig. 244). These structures in amphibians open into the mouth cavity at an extreme anterior position just behind, or posterior to the lateral vomer bones. With the development in reptiles of the secondary roof of the mouth, or "hard palate," by the growth of lateral shelves from the maxillary and palatine bones, that meet along the middle, the passage-way between the external and internal nares becomes much elongated.

With a choanal opening into the mouth it becomes possible to receive olfactory stimuli from the outside world, not only through the front door of the external nares, but also by way of the back door of the choanæ, from food substances taken into the oral cavity. Most so-called "flavors," which are associated commonly with the sense of taste, arise largely from the latter sort of olfactory stimuli, as is realized when, with a "head cold," the swollen mucous membranes largely occlude the choanal passages, and food "loses its taste."

The enlargement of surfaces for the display of epithelium within the nasal chambers, is brought about (1) by the folding of the mucous membrane which lines the chambers; (2) by the formation of *conchæ*, or shelflike extensions of the walls; and (3) by incorporation within the system of nasal passages of accessory spaces, or *sinuses*, in communication with the main nasal cavities.

The first method, of membranous duplication, is found extensively among fishes. The mucous lining of the nasal chambers

in a dogfish, for example, bears a distant resemblance to the leaves of a book because of its numerous folds. This device, however, would not be as effective out of water, for the folds would tend to adhere together when not kept separate by immersion in an aqueous medium.

In reptiles a single unrolled concha, or projection from the ectoethmoidal wall of the nasal chamber, is present on either side, being slight in turtles, but of considerable size in crocodiles and alligators. In birds the nasal chamber, compressed in accordance with the general policy of compactness that characterizes avian anatomy, has its surfaces compensatingly increased by the presence of three conchæ, the most anterior of which is located in the vestibulo-respiratory region, while the smaller middle and posterior ones, serving as a supportive substrate for the display of the sensory Schneiderian membrane, are no doubt of chief value in supplying moisture-producing area for the respiratory mechanism.

The conchæ reach their greatest elaboration in mammals, particularly ungulates, rodents, and carnivores, often becoming rolled like a scroll, thus presenting a maximum surface within a minimum space (Fig. 631). In man, whose sense of smell is inferior to that of many other mammals, the conchæ are smaller in size and reduced in number to three (Fig. 632). These are named, with reference to the particular cranial bones which give them support, the *nasoturbinals*, *maxilloturbinals*, and *ethmoturbinals*. The two former arise on either side from the lateral walls of the nasal chamber, while the latter grows out from the median ethmoidal septum, becoming insinuated between the other two (Fig. 633). The maxilloturbinals are further supported by independent skull bones, termed in human anatomy the *inferior turbinated bones*, which join the maxillary and palatine bones by means of sutures.

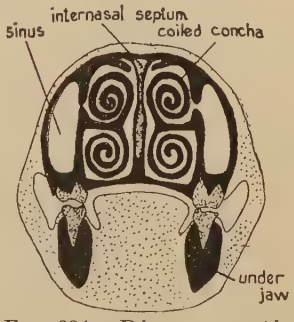


Fig. 631.—Diagrammatic cross section through the nasal region of a mammalian head. (After Boaz.)

C. Accessory Sinuses

Skeletal parts that surround the nasal region, while often appearing to be rather massive, are in reality exceedingly light and

delicate because of their spongy structure. The formation of air spaces in facial bones is carried to a remarkable extent in the large skull of the elephant, which would otherwise be uncomfortably heavy, and also in the transformations which affect the contour of the human face at about the time of puberty. In the cranial bones of mammals generally, *sinuses*, or large air spaces

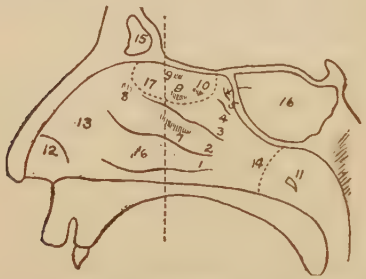


FIG. 632. — Diagram of the lateral wall of the right nasal cavity in man. *1*, inferior concha; *2*, middle concha; *3*, superior concha; *4*, first supreme concha; *5*, second supreme concha; (the apertures *6* to *10* are covered from sight by the conchæ but their position is indicated by vertical lining); *6*, aperture to the naso-lacrimal duct, opening into the inferior meatus; *7*, opening of maxillary sinus (middle meatus); *8*, opening of frontal sinus; *9* and *10*, openings of ethmoidal sinuses into the superior meatus; *11*, opening of the Eustachian tube; *12*, vestibule; *13*, atrium; *14*, choana; *15*, frontal sinus; *16*, sphenoidal sinus, whose opening is indicated by an arrow; *17*, olfactory region, whose limits are marked by the dotted line. The vertical dotted line shows the plane of section from which Fig. 633 is drawn. (After Parker.)

FIG. 633.—Diagram of a transverse section of the right nasal cavity in man, made at the plane indicated by the vertical dotted line in Fig. 632. *1*, inferior concha; *2*, middle concha; *3*, superior concha; *4*, nasal septum; *5*, inferior meatus; *6*, middle meatus; *7*, superior meatus; *8*, common meatus; *9*, olfactory cleft (left side); *10*, ethmoidal sinuses; *11*, maxillary sinus. (After Parker.)

lined with mucous epithelium, are present communicating with the nasal cavities. The principal ones of these are the *maxillary sinuses* on either side of the nose, the *sphenoidal sinus* between and below the two nasal cavities, and the *frontal sinuses* in the region of the forehead (Fig. 634). The presence of warm air, which is contained in these reservoirs, because of exposure to the capillaries of their surfaces, is an advantage, since it may be mixed with cool dry air from the outside, in this way equalizing it with respect to

temperature and moisture before it strikes the delicate olfactoreceptors, or passes on to the respiratory passages.

D. Nasal Ventilation

The circulation of water, containing dissolved gases, across the olfactory surface in the nasal pit of fishes, is effected largely by the presence of cilia. In elasmobranchs it is facilitated by a curving partition which partially subdivides each pit into an intake and an outgo region. This division is carried further in many teleost fishes, as, for example, in the conger eel, *Muræna* (Fig. 635), in that each external naris has become double, thus presenting, instead of the usual two openings, four chimney-like nostrils on the top of the head, none of which penetrates to the mouth cavity.

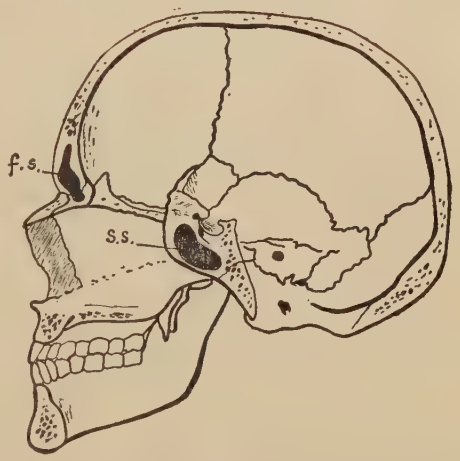


Fig. 634.—Median section of a human skull, with, *f.s.*, the frontal, and *s.s.*, sphenoidal sinuses in black. (After Spalteholz.)

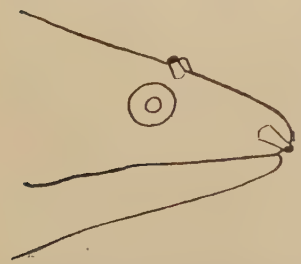


Fig. 635.—Lateral outline of the head of a fish, *Muræna*, with projecting tubular nostrils that open into a common chamber but not into the mouth cavity. (After Wiedersheim.)

With the establishment of the choanæ and the transfer of air instead of water through the nasal cavities, a system of valves and muscles becomes elaborated in connection with the breathing mechanism (Chap. XIII, Respiration), by means of which the air is kept moving. The remote situation of the Schneiderian membrane above the respiratory passage-way, makes it possible ordinarily to breathe air without stimulating the olfactoreceptors to any great extent, even when odorous substances are about, unless air is drawn in vigorously over the upper olfactory route, as in "sniffing."

Animals primarily aquatic, such as fishes and amphibians, have the olfactory membrane spreading over the entire nasal cavity,

but a differentiation into vestibulo-respiratory and olfactory regions is found in air-breathing amniotes, beginning with the reptiles. In animals secondarily aquatic, like seals and possibly whales, which have largely lost the olfactory epithelium, the nasal cavities become entirely respiratory in character.

E. Moisture-Producing Devices

Not only are sebaceous and mucous glands present in the nasal passages of land vertebrates, but a constant additional supply of moisture is also furnished by the excess of fluid from the tear glands, which is continually escaping into the nasal chamber through the lacrimal ducts at the inner angles of the eyes. This nasal flow of tears is particularly well demonstrated by a sniffling child emerging from an emotional crisis that has caused weeping.

F. Snouts and Noses

In mammals the nasal cavities may be enclosed by the fleshy tissues of a snout, or, in primates, roofed over by an external nose, but these prominent features usually have comparatively little to do with the sense of smell.

Fig. 636. — Sensitive snout of a star-nosed mole, *Condylura*. *a*, lateral; *b*, anterior. (After Gervais.)

Snouts are organs of touch in nocturnal or burrowing forms (Fig. 636), while in animals like pigs, which "root for a living," they are mechanical organs of the first order, and may even be strengthened by calcified cartilage (Fig. 637).

The moist snout of a deer or a dog might well be termed a general *anemoreceptor*, or detector of air currents, similar in function to the rheoreceptors that make aquatic animals aware of water currents, since, as every hunter knows, it is an extremely delicate apparatus for detecting the direction of air currents, and in locating odoriferous enemies or prey.

The trunk of an elephant, which is a combination of a long drawn-out nose and upper lip, is far removed from the primary olfactory function, while the external nose of man, which presents so many interesting variations, is far more useful in the expression of the emotions than as an organ of olfaction.

G. Odors

The diffusion of odorous substances through the water is very much slower than through air, yet in spite of that fact sharks are known to be able to discover a dead body at a considerable distance in a remarkably short time, although when cotton is stuffed into their nasal pits, they are unable to locate odorous food readily even in their immediate neighborhood.

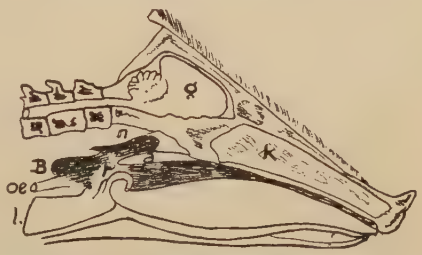


Fig. 637. — Median section through the head of a pig. *a*, soft palate; *B*, bursa pharyngea; *g*, brain; *k*, cartilaginous wall of the nasal cavity; *l*, larynx; *n*, naso-pharyngeal cavity; *oe*, esophagus; *p*, naso-pharyngeal isthmus. (From Weber, after von Lothes.)

In the open air, odors though rarely emanating in all directions equally as sound and light tend to do, are particularly influenced by air currents that may be present. Odorous gases, the farther away they are from the point of release, are not only more diluted, but also travel more slowly (Stephan's Law). Nevertheless, extremely minute quantities of certain odors are perceptible at considerable distances from their origin, as every bloodhound attests.

Allison and Katz, in *The Journal of Industrial Engineering* for 1919, give a table in milligrams of minimum concentrations of various chemicals that are perceptible in a liter of air. Among other substances, the quantity of chloroform is given as 3.3; iodoform, 0.018; propyl-mercaptan, 0.006; and artificial musk, which is by far the "smelliest" known chemical substance, 0.00004 milligrams.

Land amphibians, reptiles, and carnivorous birds, such as the vulture, depend more upon the sight of moving prey than upon the sense of smell in finding their food, while many mammals, as man, for example, are either *microsmatic*, that is, poor "smellers," or *anosmatic*, without any sense of smell at all, like the Cetacea, whose nostrils have been readjusted into a periscopic position and are entirely devoted to respiratory uses.

Most evil-smelling things are bad or poisonous, but not invariably so. Carbon monoxide gives out no olfactory warning and is very poisonous, while certain cheeses, which are decidedly repulsive in odor, are not only non-poisonous but highly nutritious.

The evolution of the olfactory lobes indicates that the sense of smell is the most animalistic of all the major senses. Its decadence human beings suffer with little inconvenience or regret.

The attempt to classify different odors has not been very successful, although the existence of several specifically different kinds of olfactory receptors, adequate only for particular odors, is quite likely. Henning in 1916 proposed six different categories of odors namely, foul, flowery, fruity, burnt, spicy, and resinous, and he arranged these primary types of olfaction theoretically at the corners of a five-sided polygon (Fig. 638). This plan has the advantage of providing a logical place on some face of the polygon for any possible intergrade between these six primary odors. Parker comments upon this clever classification as follows: "So far as an arrangement of odors is concerned, the clarity of Henning's scheme is at once its most attractive and suspicious feature."

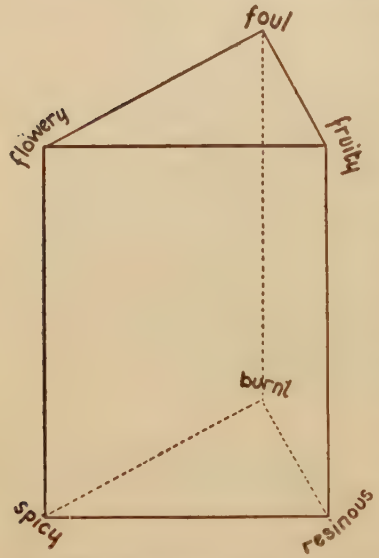


FIG. 638.—Diagram to show the relation of different odors to each other. (From Parker, after Henning.)

H. Jacobson's Organ

Among the accessory structures of the nasal apparatus is *Jacobson's organ*, which was discovered in 1811. It is a cavity, derived embryologically from the olfactory cavity, and is lined with olfactory epithelium, and supplied by the first and fifth nerves. It may remain as a common ventral diverticulum of the nasal cavities on either side, or become entirely shut off as a separate chamber, opening into the mouth by a passage-way of its own.

Such a ventro-lateral *cul-de-sac* from the nasal cavity of either side, occurs in Amphibia but does not open into the mouth cavity. It is in snakes and lizards (Fig. 639), that Jacobson's organ reaches its highest development, being reduced in turtles and crocodiles, and appearing only as an embryonic structure in birds. In mam-

mals it is likewise embryonic or degenerate in most cases, with its best representation in monotremes, marsupials, insectivores, and rodents, being entirely absent in whales, bats, and Old World monkeys.

The history of Jacobson's organ in man is entirely interuterine. Arising at the beginning of the third month as small outpocketings of epithelium in the lower part of the nasal septum, it forms a slender blind sac on either side, reaching its greatest elaboration

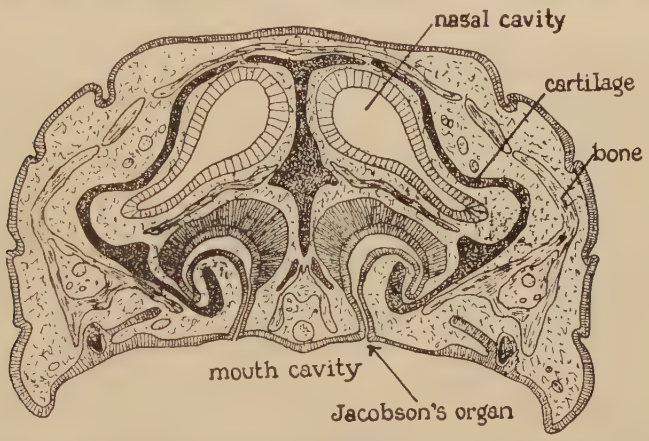


Fig. 639.—Cross section through the head of a lizard, *Lacerta agilis*, with the lower jaw removed, showing Jacobson's organ opening into the mouth cavity. (After Schimkewitsch.)

at about the fifth month. Before birth it becomes entirely reduced. This organ probably serves those animals which have it as an accessory olfactory organ for testing odorous substances held in the mouth.

2. Gustoreceptors

Just as the chemical sense of smell is located with special reference to the entrance to the respiratory passages, so the sense of taste stands as sentinel at the portal of the digestive tube, and scrutinizes all substances that enter there.

In the case of a few insects, taste is also pressed into other service than that of food testing, the female tree cricket, *Œcanthus*, for example, exuding a drop of liquid which is "tasted" by the male as a stimulating preliminary to the mating process.

A. Taste Buds

Gustoreceptors, or the sense organs of taste, are composed of clusters of cells, called "taste buds," which follow the same plan throughout the vertebrate series, differing in the various groups principally in their arrangement with relation to different kinds of *papillæ*, and in the distribution of these papillæ.

The parent tissue that gives rise to the taste buds is ectodermal in derivation. In many fishes, such as carps, sticklebacks, suckers, and catfishes, the ability to taste is not confined to the mouth cavity, but extends over the ectodermal outside of the body, even as far as the tail.

With the emergence from water to land, the gustoreceptors, are withdrawn to the moist environment of the mouth cavity which is the logical place for encountering food solutions.

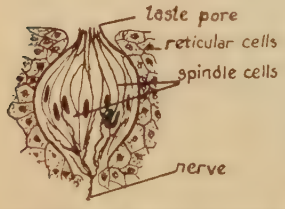


Fig. 640.—A section through a taste bud. (After Burton-Opitz.)

A typical taste bud (Fig. 640), consists of a compact group of receptor and sustentacular cells, the former of which are in contact with free nerve endings from cranial nerves. The sustentacular cells are of two kinds, namely, *basal cells*, which Rauber suggests are "understudies" held in reserve for the renewal of other cells in the cluster, and elongated *supporting cells* both peripheral and interstitial, the former curving somewhat like the staves of a barrel and giving the oval shape to the entire group.

The *sensory-receptor cells* which are slender and elongated, each with a somewhat enlarged branching basal end, terminate peripherally in a delicate protoplasmic hair or flagellum. They differ from the receptors in the lateral line organs, to which the taste buds bear a superficial resemblance, in that their ciliated ends extend all the way to the surface, meeting at a pore formed by the converging tips of the sustentacular cells, instead of projecting simply into the bottom of a cavity, as in the lateral line clusters.

The free nerve endings connecting with gustoreceptors, may be either, or both, *inter-* and *intragemmal* in character. Intragemmal fibers penetrate into the taste bud itself and lie between the gustoreceptor cells. Intergemmal fibers on the other hand, end freely outside the taste buds between unspecialized epi-

thelial cells. Both of these types of endings, which sometimes resemble a candelabrum in their multitudinous branching, come from one and the same cranial nerve fiber.

The center of the gustatory function within the brain is the *nucleus solitarius* in the medulla, connecting with neurones that take part in the formation of the *chorda tympani* branch of the seventh, and in the *glossopharyngeal*, or ninth nerve (Fig. 605). In fishes branches of the fifth and tenth nerves may also supply organs of taste.

B. Papillæ

There are four types of elevations, or *papillæ*, in the mucous membranes, which have to do with the display of taste buds, namely, (1) filiform; (2) fungiform; (3) foliate; and (4) vallate.

Filiform papillæ, are tiny threadlike or conical projections which are largely responsible for the velvety appearance of the surface of the tongue. They are not particularly associated with taste buds, although they serve to retain food solutions temporarily. In many mammals the filiform papillæ become capped over with corneal material, taking on a mechanical rasp-like character, as shown by the tongues of cats and cattle, who use this device as a hair-brush.

Fungiform papillæ (Fig. 409), are elevations from the surface of the mucous membrane that suggest the shape of a mushroom, hence their name. They are beset with taste buds, and serve to bring these chemical receptors into contact with food solutions in the mouth. Over the surface of the human tongue there may be as many as three or four hundred of these papillæ, but they are always better developed in children than in adults. They are more numerous along the sides of the tongue than elsewhere, and have the appearance of small red spots.

The *foliate papillæ* which are usually located near the base of the tongue, are tiny ridges bearing taste buds (Fig. 409). In man there are only three to eight of these ridges, but in rodents their number and size is much increased.

The most elaborated of all the modifications for the display of taste buds are the *vallate papillæ* (Fig. 641). These resemble projecting knobs, surrounded by grooves like the moat around a castle, which serve to retain dissolved food substances. In the human fetus, taste buds are distributed even over the top

of the knob, but in adults they are confined to the sunken walls of the moat, where they are not only in direct contact with solutions to be tested, but are protected from mechanical injury to which they would be liable at the surface.

Serous glands, called *von Ebner's glands*, open at the bottom of the moat and aid in keeping it filled with fluid.

Vallate papillæ are usually arranged in rows at the back of the tongue. There are two rows in monotremes, moles, bats, hares, pigs, horses, and edentates; three rows in marsupials, many insectivores, squirrels, and apes; four rows in the monkeys, *Macacus* and *Cercopithecus;* and but a single row, which is arranged in a V-shaped formation in the dog and man. They are missing in guinea pigs and coneys (*Hyrax*).

Fig. 641.—Diagram of a circumvallate papilla, showing the position of the taste-buds. (After Burton-Opitz.)

The number of taste buds to each vallate papilla varies greatly in different mammals. Hesse has estimated 480 in the sheep; 1760 in the cow; and 4760 in the pig. A cow, having about twenty papillæ, would consequently possess approximately 35,000 taste buds, while a giraffe, which is known to have over thirty papillæ, would probably prove to be still more generously endowed. In fact taste buds have their greatest development in mammals, such as ruminants, that have specialized grinding molars and retain food within the mouth cavity for a prolonged period.

Stahr has made the interesting observation that the taste buds on the tongue of the domesticated white rat are considerably reduced in number as compared with those of the wild rat.

C. Comparative Anatomy

Amphioxus has cellular structures that resemble taste buds upon the cirri around the mouth, but their function is unknown.

The sense of taste in fishes is, as already pointed out, much more generalized than in land forms, the gustoreceptors extending over the outside of the body, where they appear more as intergemmal endings than as taste buds.

Not much is known of the sense of taste in amphibians. These animals surely possess free nerve endings that serve as chemical irritoreceptors in the skin. They have groups of cutaneous

sense cells also which are, however, probably more tactile than chemical in function. Whatever sense organs may be found in the mouth have slight opportunity to be of gustatory service, since the food is swallowed at once without being held in the mouth.

In reptiles, particularly crocodiles and snakes, taste buds are located in the posterior part of the mouth cavity, which is less cornified than the anterior part.

Taste buds are present but scarce in the bird's mouth, and are situated posteriorly instead of upon papillæ as in mammals. The majority of birds with small tongues have most of the taste buds in the floor of the mouth near the lower mandibles, while birds like parrots, with large fleshy tongues, give lodgment to the gustatory organs on the tongue itself, or along the sides of the maxillary half of the beak.

In mammals the greatest elaboration of the papillæ occurs in connection with the evolution of heterodont dentition, and grinding molars. The taste buds are not confined to the tongue, but are also found on the anterior surface of the soft palate, on the epiglottis, the pharyngeal wall, and even on the inside surfaces of the cheeks.

In man there is an oval area on the dorsal surface of the tongue that is free from taste buds, as is also the under side of the tongue, although during embryonic life the *plica fimbriata*, or "secondary tongue" (see Chap. XI) that forms the underpart of the final or tertiary mammalian tongue, shows the presence of taste buds.

That the sense of taste in man is degenerating is proved not only by the fact that taste buds are more widely distributed during the fifth to seventh months of fetal life than in the adult, but also by the fact that the inner surfaces of the cheeks respond to taste far more keenly in children than in older persons.

Taste buds are either lacking in sea cows and whales, or they are represented in very degenerate form.

D. Classification

The subjective classification of gustatory sensations into pleasant, unpleasant, indifferent, or absent, is better replaced by an objective grouping according to the types of gustatory stimuli. Four such categories may be accepted as demonstrable, namely, sweet, salty, sour, and bitter. Intergrades probably occur. and there is

no doubt that confusion often results particularly with tactile and olfactory stimuli. Thus, when one speaks of a "slimy" or "gritty" taste, he is referring in reality to tactile stimulation, while the so-called "taste" of onions, or of wine, is largely a matter of olfactory stimulation.

Although indistinguishable from each other histologically, there are probably specific gustoreceptors, adequate for each of the four types of stimuli just mentioned, since, upon application of cocaine to the tongue, the sense of bitter disappears first, then that of sweet, salty, and sour in succession. The distribution over the human tongue also of the four kinds of gustation, indicates specific differences on the part of the receptors, as shown in Fig. 642, in which the result of the careful mapping of the various gustoreceptors on the human tongue, is indicated. From these diagrams it will be seen that sour receptors predominate along the edge of the tongue; salty, both at the tip and at the edge; bitter, at the base; and sweet, at the tip.

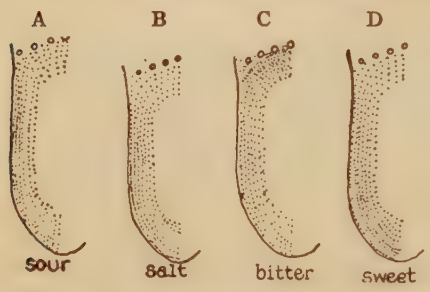


FIG. 642.—Diagrams of the right half of the human tongue, illustrating the distribution of the taste buds. The dots represent the area and concentration of a given sense of taste. *A*, the sour taste, concentrated on the edge; *B*, the saline taste, at the tip and on the edge; *C*, the bitter taste, at the base; *D*, the sweet taste, at the tip. (Modified from Hänig, after Parker.)

V. THE MASTER SENSES

1. Phonoreceptors

A. Stato-Acoustic Organs

Although equilibration and hearing are two quite distinct functions, the *stato-acoustic organs* through which they are mediated in vertebrates are so intimately associated in structure and derivation, that they must be considered together. The same is not true of invertebrates generally in which the sense organs for regulating equilibrium, when present, are distinct and independent from those for receiving sound waves.

The function of equilibration is unnecessary and absent in

plantlike animals, like hydroids and corals, which remain attached in one position, but in locomoting animals that must maintain their bodies in various positions by their own efforts, there are three general types of equilibrium, namely, indifferent, stable, and labile.

Indifferent equilibrium is uncommon, and involves no sense organs. It may be seen, for example, in the Heliozoa, which are minute spherical protozoans that hang suspended any side up in water.

Stable equilibrium, that also does not require the aid of sense organs, applies to inert as well as living bodies. A flounder, coming to rest on one side, like a bicycle laid down upon the ground, illustrates what is meant by stable equilibrium.

An animal like a dog standing "on all fours," or a man balanced upon two legs, on the other hand, whose center of gravity is too high to allow balancing without muscular effort, exhibits *labile equilibrium*. This type of equilibrium involves biological factors within the body, as well as the physical pull of gravity without, for not only must a tension be maintained between opposing muscles to prevent collapse, but a coördinating nervous apparatus, including sense organs, is necessary to mediate between an organism and the environmental setting in which it finds itself.

1. Statoreceptors

In lower free-swimming animals the sense organs of equilibrium are *statoreceptors* of various sorts, depending for their action upon differences in the pressure of a comparatively heavy, secreted mass, *statolith*, which is brought into contact with sensory receptor cells, whenever there is a change in the position of the body.

Around the edge of a floating jellyfish at the base of the tentacles, for example, there may be arranged a row of *statocysts*, each consisting of a bell-like structure lined with sensitive cells and containing a pendulous "clapper," which is made heavy by the deposition of limy salts in its end (Fig. 643). Whenever these fragile medusæ, in the course of their aimless voyagings upon the surface of the ocean, are tipped up at an unusual angle by the force of a wave or by any other outside agency, the tiny loaded clappers within the statocysts swing over and strike the sensory cells upon one particular side of the bell, with the result that the jellyfish rights itself sufficiently to bring the swinging clappers to a stand-

still, thus restoring equilibrium. If the statocysts halfway around the margin of a jellyfish are carefully dissected off or destroyed in any way, the animal is no longer able to right itself, but floats in an unnatural attitude in the water.

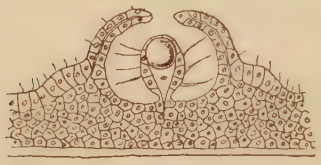


Fig. 643.—Statocyst of a medusa, *Rhopalonema*, consisting of a weighted "clapper," supplied with sensitive "hairs," within a sensory bell. (After Hertwig.)

Equilibratory mechanisms, presenting various modifications embodying this fundamental idea, occur not only in free-swimming cœlenterates and arthropods, but also in various other invertebrates.

Among vertebrates the function of equilibration is accomplished not so much by static organs alone, as through the coöperation of several sense organs, primarily devoted to other purposes. Thus, a man maintains his upright posture without collapsing through the interaction of (1) the tangoreceptors upon the soles of the feet, which are in contact with the ground; (2) the sense of sight, which informs and reassures him of his relation to his surroundings; (3) the proprioceptive "muscle sense," that attends to the proper tension of opposing muscles; and finally (4) nerve endings from the acoustic (VIIIth) nerve, connecting with the semicircular canals of the ears, which have a function much like that of the statoreceptors of the invertebrates.

If for any reason any one of these four factors is withdrawn, temporarily or permanently, equilibrium is either upset or maintained with difficulty.

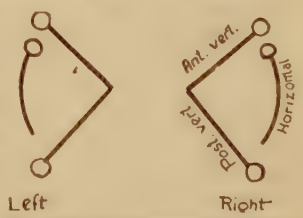


Fig. 644.—Diagram to show the relation of the semicircular canals and their ampullæ to each other.

2. Semicircular Canals

The *semicircular canals* are embryologically inseparable from the vertebrate ear, and their origin, structure, and arrangement will be more fully considered in a later paragraph in connection with the ear. It is only necessary here to point out that they are typically three in number, that they are placed approximately at right angles with each other in the three planes of space (Fig. 644), and that there is a bulblike enlargement, or *ampulla*, at one end of the fluid-filled semicircular tubes. These ampullæ are static organs,

responding to stimuli of differential pressure. A group of receptor cells, bearing stiff hairs which project into the cavity of the ampulla (Fig. 645), and connect with a branch of the VIIIth nerve, form a device which is stimulated by the movement of the fluid (*endolymph*) contained within the tube, whenever the apparatus is tipped into a new position. Since the semicircular canals occupy three different planes, the combined stimuli received by all the three ampullæ make it possible to detect any shift in position, and so to initiate the muscular responses appropriate for the maintenance of equilibrium.

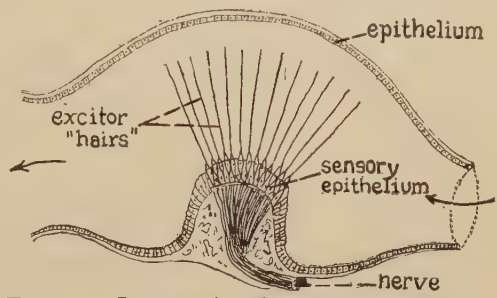


FIG. 645.—Long section through the ampulla of a fish, *Gobius*. (After Hensen.)

Otoconia, which are either crystals or concretions of calcium salts, may be secreted in the ampullæ and become attached to the projecting hairs of the receptor cells, thus weighting them so that the movement of the endolymph within the canals is registered with greater delicacy (Fig. 646).

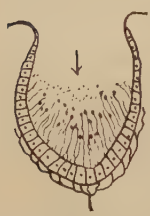


FIG. 646.—The otolithic cavity, showing the lining cells with their hairlike projections and the otolithic granules adhering to them. (After Burton-Opitz.)

Within the statoreceptor apparatus of the ear in fishes similar limy concretions may acquire considerable size, when they become known as *otoliths*, or "ear stones." These otoliths may be used to determine the approximate age of individual fishes, since they show lines of growth, resembling the rings of growth in the woody trunk of a tree.

The statoreceptor mechanism of the semicircular canals does not present any great amount of variation throughout the vertebrate series, except in cyclostomes. The hagfish, *Myxine*, has a single semicircular canal with two ampullæ, while the lamprey, *Petromyzon*, has two canals, the third horizontal one being missing, a condition that is probably more degenerate than primitive, owing to the semi-attached habit of these parasitic animals.

The peculiarly erratic movements of the so-called "Japanese dancing mice" are correlated with defective statoreceptive organs, or semicircular canals.

3. Weber's Organ

A peculiar sense organ, called Weber's organ, is found only in connection with the stato-acoustic organ of certain physoclistous fishes, whose swim bladder has lost its duct leading to the pharynx by means of which its hydrostatic function is effected. As the pneumatic duct disappears the two endolymphatic ducts of the membranous labyrinth form a sinus, connected with the closed swim bladder by a row of small ossicles. The result is a hydrostatic device which brings about a muscular reaction upon its walls through stimulation by way of the ear, thus modifying the tension of the gaseous contents of the swim bladder, and serving to adjust the position of the fish in the water.

B. The Vertebrate Ear

Hearing consists in the reception and interpretation of stimuli caused by vibrations of material particles. For this purpose auditory sense organs have been evolved, first among lower forms that are submerged in water. Later these organs become of greater importance after emergence into the rarer medium of air.

The lateral line organs, or rheoreceptors already mentioned, take the place to a considerable extent of organs of hearing in fishes, since the currents produced by moving water, and the disturbances of slow vibrations, rather than "sounds," are the most important environmental changes to dwellers in the silent aquatic world.

No doubt to many transitional, thigmotactic animals, particularly amphibians, whose bodies are not yet elevated by means of supporting legs from contact with solid earth, the vibrations which are of the greatest service, and for which their sense organs are especially adapted, are seismic rather than auditory in character. It is mostly vibrations which pass through air, however, that are concerned with the true sense organs of hearing. In this rarer medium, through which sound waves pass more slowly and with less intensity than through the denser media of water and earth, it becomes the task of evolution to elaborate intensifying and collecting devices of various sorts to supplement the sensory auditory receptors.

So it comes about that the auditory apparatus of the higher land vertebrates consists not only of a sensory receiving apparatus, the *inner ear*, but also of a *middle*, and an *outer ear*, whose supplementary function is primarily the collection and amplification of vibrations from the air.

Of these three "ears" the inner ear alone is essential and present in all vertebrates that hear. In amphibians, a middle ear is added, although it is incorrect to call it that until the outer ear, which begins with reptiles and reaches its greatest elaboration in mammals, is developed.

In describing the vertebrate ear it may be well to consider the simpler accessory parts first, and the more complicated and essential parts of the inner ear last, following the path taken by sound vibrations as they reach the listening animal.

Fig. 647.—Pinna of a human ear. (After Cunningham.)

1. The Outer Ear

The outer ear consists of a projecting flap, *pinna*, with its *muscles*, and an *auditory canal*. The pinna in man is a peculiarly moulded, flat, skin-covered, elastic cartilage, with a cuplike depression, the *concha*, in the center, surrounding the opening into the auditory canal.

This opening is guarded on either side by two projections, the *tragus* and *antitragus* (Fig. 647). In man the lower end of the ear, or *lobule*, is fleshy, pendulous, and without cartilaginous support, while the upper curving edge, or *helix*, often presents an appearance suggesting animal ancestors (Fig. 648). Embryologically it actually passes through stages resembling the ears of catarrhine monkeys and apes, before finally attaining its characteristically human outline.

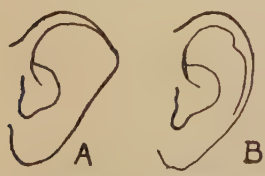


Fig. 648.—Outlines of two ears. *A*, monkey, *Macacus; B*, a human pinna, showing "Darwin's point," which is an infolding that resembles the projection on the pinna of the monkey's ear. (After Schwalbe.)

The pinna on either side of the spiracular cleft, which becomes the locus of the auditory canal, arises originally as six elevations three of which are borne by the mandibular, and three by the hyoid arch (Fig. 649).

Pinnæ become degenerate in aquatic and burrowing animals,

such as seals and moles, where they would serve no good purpose and might even be a disadvantage, but they are large in animals like bats, that are active at night or in twilight; in fast runners of the open spaces, such as deer and antelopes; and in arboreal animals, like squirrels, whose eyes, which the large ears protect to a certain extent, are exposed to chance encounters with branches and twigs.

The external ears of bats are provided with tangoreceptors to aid in avoiding obstacles during crepuscular activities, but for the most part pinnæ are principally useful in catching the *direction* from which sound waves come. To this end many animals have pinnæ that are movably hinged to the skull, and supplied with muscles so that they may be easily directed to detect the source of sounds without the inconvenience of turning a heavy head.

Fig. 649.—Embryonic stages in the development of the pinna. *1*, tragus; *2,3*, helix; *4,5*, anthelix; *6*, antitragus; *1,2,3*, elevations of mandibular arch; *4,5,6*, elevations of hyoid arch; *A.F.*, auricular fold; *o.v.*, otic vesicle. (After Arey.)

The *ear muscles* are under the control of the will. They are *intrinsic*, within the pinna, and without, *extrinsic*, connecting the pinna with the skull, thus effecting the movement of the external ears (Fig. 536). In many breeds of domestic animals, as for example, pigs, sheep, goats, dogs, and rabbits, "lop ears" sometimes develop, that lack much by way of muscular control as contrasted with upright hinged pinnæ. In the security which comes with domestication, these animals have lost something of the alertness that is the salvation of wild animals. Elephants are perhaps the only wild forms with nonerectile pendulous ears, but the self-confidence that goes with their dominant size no doubt makes the direction from which hostile noises come, a matter of comparative indifference to them.

The *auditory canal* is the external passage-way that leads to the middle ear. In man it is about 2.5 centimeters long, slightly bent, and larger at either end than in the middle. For the external third of its length its walls are kept rigid by cartilage, continuous with that of the pinna, while for the remainder of the way, they become bony, forming a part of the temporal bone of the skull, in which both the middle and inner ears are housed.

The auditory canal is lined with skin, and is supplied with *wax-glands* and outward-projecting hairs, both of which are devices that serve not only as dust arresters, but also for the discouragement of crawling and flying insect explorers.

2. The Middle Ear

On either side a *middle ear*, or *tympanum*, in the form of an irregular air-filled chamber is hollowed out of the temporal bone, between the external auditory canal and the inner ear.

A deep recess, the "attic," or *epitympanum*, communicates with mastoid "cells," or spongy cavities in the mastoid process of the temporal bone (Fig. 650), and below the *Eustachian tube* opens into the pharyngeal cavity (Fig. 651).

Fig. 650.—A section through the mastoid process, showing the spongy character of the bone.

Across the inner end of the auditory canal and separating it from the middle ear, is the "ear drum," or *tympanic membrane*, stretched within a bony frame, the *annulus tympanicus*. The ear drum is set obliquely across the passage-way of the auditory canal, and thus a larger ear drum, with a greater expanse of surface, is exposed to vibratory stimuli than would be possible if it extended squarely across.

On the face of the wall opposite the ear drum, and next to the inner ear, are two windows, the *fenestra vestibuli* and the *fenestra cochleæ*, similarly curtained by drumhead-like membranes, so that the middle ear bears some resemblance to a hollow drum, with very small membranous heads at the two ends.

The tympanic cavity in land forms is derived from the ancestral spiracle of elasmobranch fishes, that lies between the mandibular and hyoid arches, but which, in forming the middle ear, never breaks through to the outside. The intervening "skin," that remains at the outer end of the spiracular cleft, becomes the ear drum, while the other end extends to the pharynx as the Eustachian tube. Thus, the ear drum is a membrane, made up of an ectodermal layer on the outside, and an entodermal layer on the inside.

The Eustachian tube is the ventilator of the tympanum. It is broader at the pharyngeal than at the tympanic end, and re-

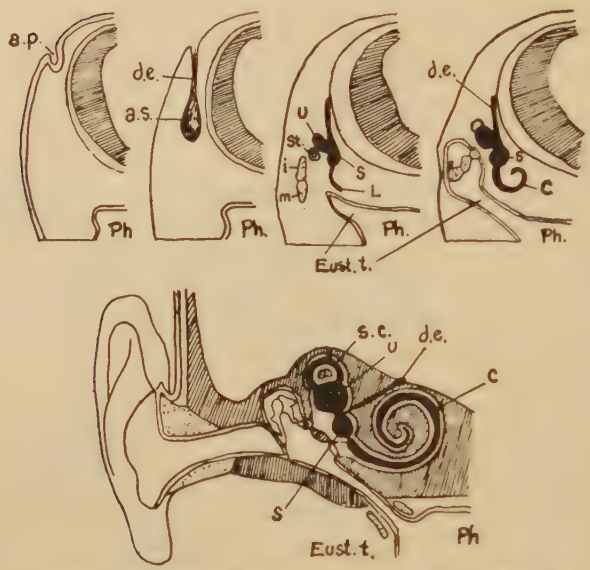


Fig. 651.—Diagrams of stages in the development of the ear. *a.p.*, auditory pit; *a.s.*, auditory sac; *c*, cochlea; *d.e.*, ductus endolymphaticus; *Eust.t.*, Eustachian tube; *i*, incus; *L*, lagena; *m*, malleus; *Ph*, pharynx; *s*, sacculus; *sc*, semicircular canal; *st.*, stapes; *u*, utriculus. (After Brandt.)

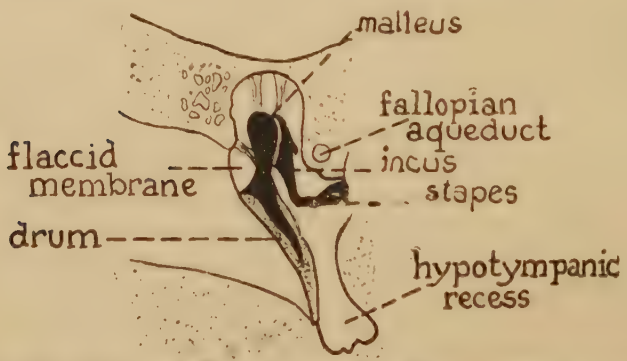


Fig. 652.—Ear bones within the tympanic cavity. (After Rouvière.)

mains closed, except during the act of swallowing, when it may open sufficiently to permit an exchange of air within the tympanum. In this way the pressure of the air within the tympanic cavity is so adjusted that it is the same as on the outside of the ear drum.

The sound waves which impinge upon the tympanic membrane are handed on across the tympanic cavity to the inner ear, and intensified during their passage by means of a chain of tiny ear bones, the hammer (*malleus*), the anvil (*incus*) and the stirrup *stapes* (Fig. 652). The malleus is attached to the inner face of the ear drum by its "handle," while the stapes, which is articulated to it by means of the intervening incus, fits into the membrane of the *fenestra tympani*, and, somewhat like the plunger of a piston, transfers by a thrust to the inner ear the sound vibrations that strike the drum.

In amphibians, instead of a chain of three bones, there is a single rodlike *columella*, extending from the ear drum directly

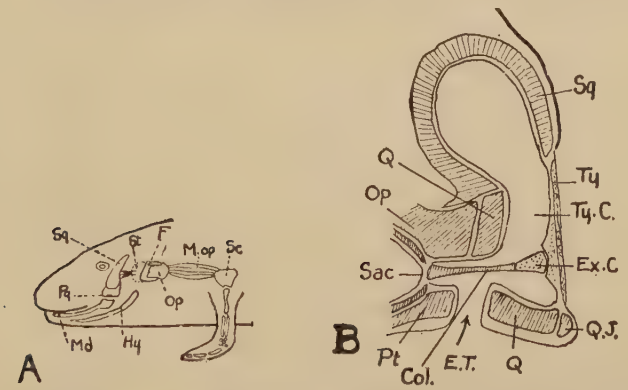


FIG. 653.—Ear bones. *A*, *Urodeles*. *F*, foot-plate of columella; *Hy*, hyoid; Md; mandible; *M.op*, opercular muscle; *Op*, operculum; *Pq*, pterygo-quadrate; *Sc*, scapula; *Sq*, squamosal; *St*, stapes, or columella. (After Kingsbury and Reed.) *B*, *Turtles*. *Col.*, columella; *E.T.*, Eustachian tube; *Ex.C*, extra-columella; *Op*, opisthotic; *Pt*, pterygoid; *Q*, quadrate; *Q.J.*, quadrato-jugal; *Sac*, sacculus; *Sq*, squamosal; *Ty*, tympanic membrane; *Ty.C.*, tympanic cavity. (After Plate.)

to the *fenestra vestibuli* (Fig. 653, A). This device forwards vibrations from the drum to the inner ear with equal power and amplitude, instead of with an increased thrust and lessened amplitude, as is the case with the chain of ear bones of mammals.

In reptiles and birds there may be two parts of the columella, either jointed or fused with each other (Fig. 653, B). The inner element, which is homologous with the stapes of mammals, is the *plectrum*, while the outer part, close to the drum, is called the *extra-columella*.

In monotremes and marsupials the stapes remains cylindrical and solid at the enlarged inner end, like a pestle, but in other mammals its enlarged end is pierced by a hole, through which a blood vessel passes, so that it takes on a fancied resemblance to a stirrup, hence its name.

Two tiny muscles within the tympanum, the *tensor tympani*, attached to the malleus, and the *stapedius*, which is fastened to the stapes, regulate the tension of the tympanic membrane and the contact between the ear bones, thus serving to increase the reception of weak vibrations, or to prevent disastrous consequences from the impact of sounds of unusual intensity.

The ear bones have a dramatic origin, being made over from skeletal elements of the splanchnocranium that formerly were put to quite different uses.

The amphibian columella corresponds to the *hyomandibular* bone of fishes, that is, the most dorsal element of the hyoid arch. The inner end of the columella is homologous with the stapes of the mammalian ear. The malleus and incus, which are peculiar to mammals, are derived from the *articular* bone of the primitive lower jaw, and the *quadrate* bone of the original upper jaw respectively (Fig. 466). Thus, mammals may be said to hear through the jaw bones of their phylogenetic ancestors.

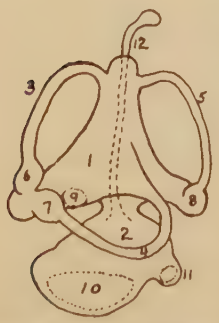


Fig. 654.—Diagram of the left membranous labyrinth of a vertebrate ear. *1*, utriculus; *2*, sacculus; *3*, *4*, *5*, the semicircular canals with their ampullæ (*6*, *7*, *8*); *9*, macula utriculi; *10*, macula sacculi; *11*, macula lagenæ; *12*, endolymphatic duct. (After Wiedersheim.)

3. The Inner Ear

The *inner ear*, which contains the essential parts of the phonoreceptive sense organs, is a closed ectodermal sac, the *membranous labyrinth* peculiarly shaped and so called on account of its complicated structure (Fig. 654). It is filled with a fluid, *endolymph*, and surrounded by a skeletal case, the *bony labyrinth*, hollowed out of the dense petrosal part of the temporal bone.

The bony labyrinth duplicates the irregular contours of the membranous labyrinth, and likewise contains a fluid, the *perilymph*, which fills the space between the two labyrinths.

In the wall of the bony labyrinth next to the tympanum are two windows, the *fenestra vestibuli* and the *fenestra cochleæ*, which

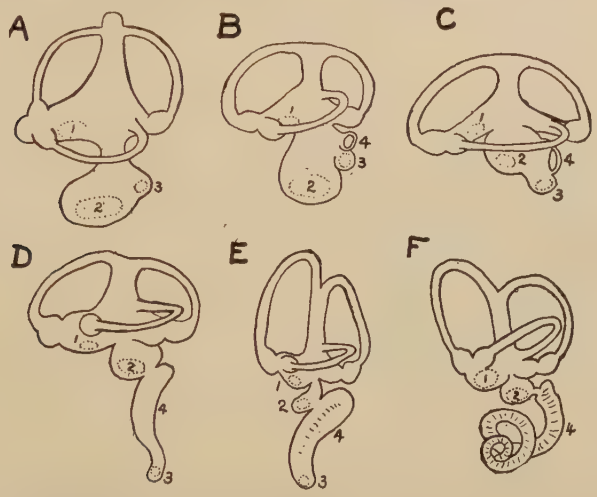


Fig. 655.—Diagrams of the left labyrinth of the ear of, *A*, a teleost; *B*, a frog; *C*, turtle; *D*, crocodile; *E*, bird; *F*, mammal. *1*, macula utriculi; *2*, macula sacculi; *3*, macula lagenæ; *4*, basal papilla. (After Hesse.)

are covered over by thin membranes during life, thus making the bony, as well as the membranous labyrinth a closed cavity.

Fig. 656. — Cross section through the cochlea. (After Burton-Opitz.)

The labyrinths consist of a *utricular region*, of which the statoreceptive *semicircular canals* are a part, and a *saccular region*, that in mammals is drawn out into a spirally-wound *cochlea* (Fig. 655, F).

In the utricular region the membranous labyrinth is closely surrounded by perilymph in which it floats, partially supported by connective tissue fibers. In the region of the cochlea, on the other hand, the inner membranous sac is in direct contact with its bony envelope along one side, and thus is not entirely surrounded by intervening perilymph.

The perilymphatic space in the cochlea is divided into two chambers by the *basilar membrane* upon which rests the membranous labyrinth of the cochlea, and the *lamina spiralis*, that projects from the inner wall of the bony labyrinth. The perilymphatic cavity below the partition thus formed, is the *scala tympani*, and the one above is the *scala vestibuli*, while the endolymphatic cavity within the membranous labyrinth is the *scala media* (Fig. 656). A thin part of the wall of the membranous labyrinth, separating the scala media from the scala vestibuli, is called *Reissner's membrane*. At the tip of the coiled cochlea the scala tympani and the scala vestibuli become continuous with each other in a passage-way called the *helicotrema* (Fig. 657), while the scala media ends blindly.

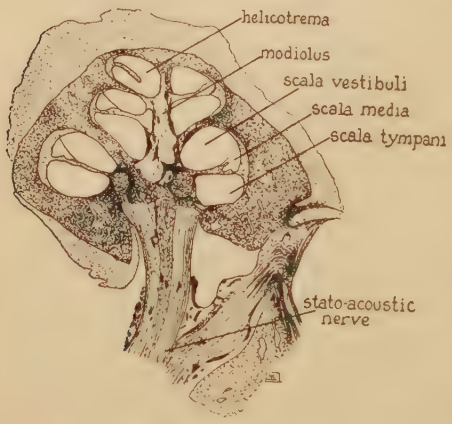


Fig. 657.—Axial section through a decalcified cochlea of a new-born child. (After Toldt.)

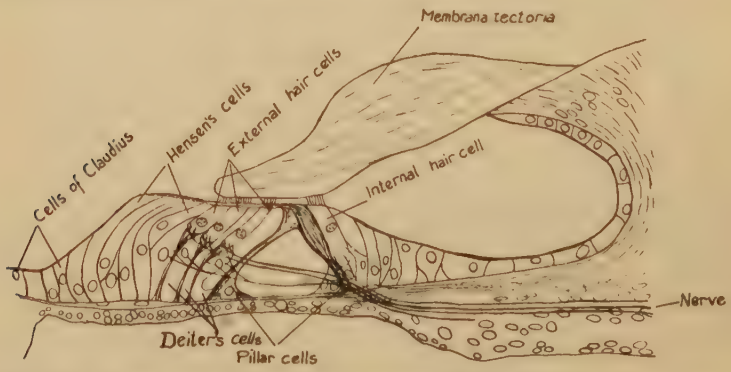


Fig. 658.—Cross section through the *organ of Corti* within the membranous labyrinth (*scala media*.) (After Szymonowicz.)

Inside the scala media, and running lengthwise along the basilar membrane, are five rows of sensory "hair cells," connected by way of the lamina spiralis with neurones which constitute

a part of the auditory (VIIIth) nerve, extending to the brain (Fig. 658). These hair cells are the specific phonoreceptors of the entire auditory mechanism. They are surrounded and supported by various supplementary cells, the whole apparatus being termed the *Organ of Corti*, in honor of Alphonso Corti (1822-76) who first discovered in 1851 these microscopic details of the inner ear.

The fenestra vestibuli is located at the larger end or base of the scala vestibuli, so that when the stapes of the middle ear, moved by sound waves which come to it by way of the ear drum, plunges back and forth against the membrane stretched across the fenestra vestibuli (Fig. 659), the vibrations are communicated to the perilymph within the scala vestibuli, and are then transmitted through the thin Reissner's membrane to the endolymph within the scala media, where they encounter the hair cells which pass on the impulse, by way of the auditory nerve, to the brain (Fig. 660).

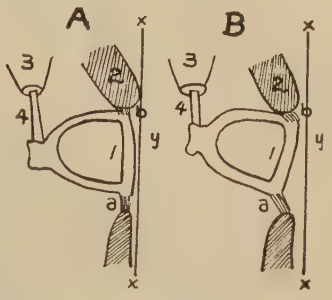


Fig. 659.—Schematic representation of the displacement of the stapes, due to the contraction of the stapedius muscle. *A*, stapes in repose; *B*, stapes during contraction of the stapedius muscle. *1*, base of the stapes; *2*, anterior border of the fenestra vestibuli; *3*, pyramid; *4*, tendon of stapedius; *a*, anterior portion of annular ligament of stapes, longer than, *b*, the posterior portion of same ligament; *x–x*, antero-posterior diameter of fenestra vestibuli, passing through base of resting stapes; *y*, point of passage of vertical line which represents axis of rotation of stapes. (After Testut.)

The membrane stretched across the fenestra cochleæ acts as a safety valve for the vibrations set up in the incompressible perilymph that is confined within the rigid walls of the bony labyrinth. Since the fenestra cochleæ is located at the base of the scala tympani, its membrane vibrates back and forth as the sound waves reach it, received by way of the helicotrema from perilymph in the scala vestibuli, thus allowing the force to die away gradually.

The hair cells of the organ of Corti, which are variously estimated from 13,000 to 54,000 in the human ear, are arranged along the basilar membrane in two bands, separated from each other by supporting *pillar cells* that lean against each other, forming an archway (Fig. 658). The inner band consists of a

single row, while in the outer band there are four parallel rows, with supporting *Deiter's cells* inserted between, holding them apart. The hair cells all increase in size toward the tip of the cochlea. Outside the outer band are the sustentacular *cells of Hensen*, grading down into the *cells of Claudius*, to form the peripheral wall of the scala media and becoming continuous with Reissner's membrane, which partitions the latter off from the scala vestibuli.

FIG. 660.—Diagrammatic section through the inner ear of man, showing by arrows the course of vibrations in the perilymph. *1*, tympanic cavity; *2*, Eustachian tube; *3*, incus; *4*, stapes; *5*, vestibule of internal ear, filled with perilymph; *6*, utriculus; *7*, central canal of cochlea; *8*, scala vestibuli; *9*, sacculus; *10*, endolymphatic duct between sacculus and utriculus; *11*, ampulla of semicircular canal; *12*, canalis reuniens; *13*, scala tympani; *14*, helicotrema; *15*, fenestra tympani. (After Burton-Opitz.)

Extending over the hair cells from the lamina spiralis, is a thin projecting flap, the *membrana tectoria*, which probably lightly impinges upon the upright hairs whenever the perilymph, in which it floats, is agitated. Thus, sound waves, which begin at some sonorous point of origin as material particles of air hitting one upon another, are changed into waves of lymph particles, that in turn are translated into nerve impulses, and finally reach the brain to be interpreted as sound.

Vibrations without definite wave length that fall irregularly upon the ear, are "noises," while vibrations repeated with exact regularity, are "tones." The *amplitude* of the vibrations determines the *loudness* of the tones produced, while the *pitch*, whether it be high or low, is correlated with the *frequency*, or the relative number of vibrations in a unit of time. The *quality*, or timbre, of a tone, by which the difference between the human voice and a violin, for example, is detected when producing the same musical note, is dependent first upon the *character*, or shape of the sound waves involved, and second, upon the "overtones," or accompanying sympathetic vibrations of differ-

ent harmonious nodal lengths, which may be added to the fundamental tone.

The organ of Corti is not the only terminus for the auditory nerve within the membranous labyrinth. There is a *crista*, or group of sense receptors supplied by the VIIIth nerve, in each of the three ampullæ of the semicircular canals, and in addition, three cushion-like patches of sensory endings, the *macula utriculi*, and the *macula neglecta* in the wall of the utriculus, and the *macula sacculi*, in that part of the sacculus which is not drawn out to form the cochlea (Fig. 661). The macula neglecta, which is double in some fishes, is absent in mammals, including man.

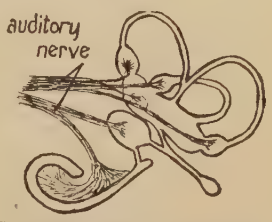


Fig. 661.—Diagram to show the endings of the statoacoustic (VIII) nerve in the membranous labyrinth and cochlea. (After Huxley.)

The inner ear is primarily a static organ, placed at the anterior end of the lateral line system, and probably derived from it. Like the pits of the lateral line it is an ectodermal invagination, appearing as an isolated vesicle on either side of the head about opposite the anterior end of the myelencephalon. As it sinks below the surface it leaves an *invagination canal*, which at first remains open to the outside but later is closed off, thus making the vesicle of the future inner ear a completely closed sac, surrounded by mesodermal tissues.

By constriction this sac is next marked off into an utricular and a saccular portion, at the utricular end of which the walls become pinched together into three flattened semicircular folds, placed approximately at right angles to each other. At the central point, where the inner surfaces of these walls are brought into contact with each other by the pinching process, absorption occurs, leaving behind the three loops of the semicircular canals without destroying the continuity of the cavity within the sac or allowing it to break through to the outside.

Meanwhile the utriculus, which at first is nothing more than an accessory reservoir for the endolymph employed in the semicircular canals, sprouts out an elongation, the *lagena*, which eventually becomes the coiled *cochlea*, with an auditory rather than a static function (Fig. 662).

In land vertebrates, at the same time that the inner ear is thus coming into its own, the tympanum or air chamber of the middle

ear is being formed close by out of the ancestral spiracular pouch, or cleft, while, with the elaboration of the secondary jaw apparatus, certain relics of the primitive splanchnocranium, having lost their original employment as skeletal mouth parts, move into the middle ear chamber to assume the new rôle of ear bones.

A parallel to the development of the ear in the individual, is found in the evolution of the ear in the different classes of vertebrates.

There is no ear in amphioxus. Among cyclostomes the membranous labyrinth in *Myxine* is a simple undifferentiated sac with a single semicircular canal. In *Petromyzon* two canals are present,

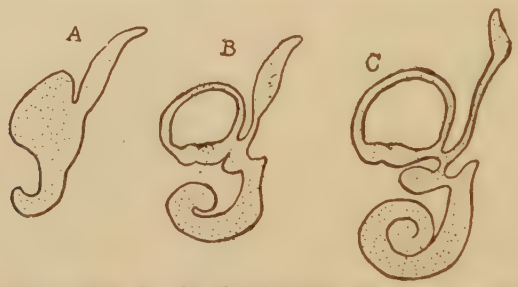


FIG. 662.—Three stages in the development of the human membranous labyrinth. *A*, at the end of the fourth week; *B*, at the end of the sixth week; *C*, at the end of the tenth week. (After Streeter.)

with a constriction in the sac that indicates the beginning of a sacculus. A *macula communis* in the saccular end, along with a *crista* in each ampulla, represents the nerve terminals.

In fishes generally the ear hardly rises above the static function of equilibration. There are three well developed semicircular canals and a primitive sacculus, frequently provided with a large otocyst, or "lucky bone," which is surely more static than auditory in function. It is extremely doubtful whether fishes can "hear," although they respond readily to certain types of jarring or vibration by means of their lateral line organs. Whatever vibrations from the surrounding water reach the labyrinth of the ear do so directly through the skull. In the elasmobranchs and some ganoids the spiracular opening still further exposes the inner ear to external stimuli, but no middle or outer ear is elaborated.

There is another reason why fishes are probably oblivious to sounds borne on the air, and that is that, although sound waves transferred in water or through solid objects, as a telegraph wire for

example, travel much faster than in air, it is very difficult for vibrations to pass readily from thin air into the denser medium of water.

In elasmobranchs according to Wenig, Fineman, and others, the invagination duct remains open, although in most fishes and higher forms it is closed, and another but somewhat similar prolongation of the membranous sac, the *ductus endolymphaticus*, develops, which ends blindly.

In some of the higher amphibians, as frogs and toads, but not in the Apoda or the Urodela, the spiracular canal enlarges into a tympanic cavity, which is not properly a "middle ear" since no outer ear is present. A large external ear drum, connected by a columella and a cartilaginous *operculum* with the fenestra vestibuli in the wall of the inner ear, is placed at the level of the skin, and is consequently much exposed to injury.

The first true auditory nerve terminals appear in the Amphibia, in the form of the *macula neglecta* and the *papilla basilaris*, the latter of which is of greater importance since it becomes the sensory receptor within the cochlea when that structure develops from the sacculus. The macula neglecta continues to be represented in reptiles and birds, but disappears in mammals.

The ear drum is sunken in reptiles and birds, forming a pit which is the beginning of the external auditory canal. Some lizards and the crocodilia have an ear fold at the margin of the pit, which foreshadows the pinna of the mammalian ear. By means of this fold an alligator can close the auditory canal while submerged in water. "Horned" owls and certain other birds have the ear fold supplemented by feathers.

The tympanum of snakes and legless lizards is much reduced or absent, as direct contact with the ground is the means employed for the reception of seismic vibrations on the part of these thigmotactic animals.

In birds and crocodiles the two Eustachian tubes form a median duct that enters the mid-dorsal region of the pharynx by a single opening.

In the inner ear of reptiles and birds the curving lagena becomes the auditory center (Fig. 655), while in mammals the lagena curves still more to form the compact, space-saving cochlea. The degree to which the cochlea is coiled in various mammals is as follows: *Echidna*, ½; whale, 1½; horse, 2; rabbit, 2½; man, 2¾; cat, 3; cow, 3½; pig, 4; South American "paca" (*Cœlogenys*), 5.

The development of the two saculæ (vestibuli and cochleæ) in the bony labyrinth of the mammalian ear, whereby the waves of the perilymph are confined to a definite path, and the establishment of the fenestra cochleæ as a safety valve are further mammalian refinements. The malleus and incus of the middle ear are also added in the mammals, while the auditory canal of the outer ear becomes elongated and bent, thus affording greater protection to the ear drum.

A favorable conjunction of various preliminary factors has given to higher animals the wonderful gift of hearing. First, in the struggle for existence a more effective ability to "bite," forced the strengthening of the jaws, which entailed a securer anchoring of the upper jaw directly to the cranium instead of its secondary suspension from the skull by means of the hyomandibular apparatus. As a consequence of the release of the hyomandibular bone, the upper jaw was left free to become transformed into the columella, or the stapes. Next, the rise of the secondary investing jaw bones and the formation of the hard palate, allowed for the transformation of the proximal ends of these primitive and temporary jaws, now rendered superfluous in their former capacity, into the malleus and incus.

Finally, the accidental circumstance that air contains about thirty times as much oxygen as water, made it inevitable that certain pioneer animals, the Dipnoi and Amphibia, should rise to lead the vertebrate hosts out of the bondage of a watery environment into the promised land of air, whereby the spiracular canal became a sound-transferring, instead of a respiratory device.

When it is remembered that the evolution of hearing has had as a corollary, voluntary voice production, involving not only the mating calls and warning cries of higher animals, but also human speech upon which the culture of man rests, it is evident that the transition from water to land, which initiated and compelled these developments, is one of the most important turning points in the history of living things.

2. Photoreceptors

The most important and far-reaching of all the sensory avenues of knowledge concerning the external world, is through the sense of sight. Most of the other senses, such as taste, smell, touch, and temperature receptors, furnish information only con-

cerning the immediate environment. It is true that the radius from which the impressions arrive is much enlarged by the sense of hearing, but hearing is confined to geographical distances, even when augmented by the marvelous mechanical extensions that are made possible by radio apparatus. What an infinitude of space is comprehended in the statement that *one can see a star!* Although one must travel in order to see distant lands that lie beyond the horizon, as well as to come in contact with distant stimuli of any sort, it is quite possible to stand still upon a starry night and *see* the heavenly bodies that mark the very outposts of the known universe.

None of the human senses is so sorely missed as sight. After Beethoven became deaf and could no longer receive in tones the musical harmonies which teemed in his fertile brain, and which were all the world to him, he became an object of sympathy, but a blind astronomer, living upon the memories of what he can no longer see, is surely a sadder figure.

Nevertheless, sight is by no means a universal or indispensable endowment of animals, for many creatures are sightless, and "love darkness rather than light."

Although all organisms are, either directly or indirectly, dependent upon the light of the sun, and upon green plants which are able by photosynthesis to utilize the energy of sunlight, it is not always necessary for so elaborate a sense organ as the eye to be involved in reactions to light. *Photoreceptors*, which are structures adequate to respond to the stimulus of light, include much more than "eyes." In fact, probably all protoplasm is more or less sensitive to light and the function of sight may be regarded simply as a specialized extension of this particular type of irritability.

A. Photoreceptors That Are not Eyes

If the eyeless earthworms did not retire to the safety of their burrows at break of day, after their nocturnal wanderings, the proverbial "early bird" would quickly eliminate them in the struggle for existence. They are able, however, by means of certain specialized photoreceptive cells in the skin (Fig. 126), to distinguish light from darkness and so usually escape this fate.

Many of the Protozoa, as well as larval forms of metazoan animals in which the cellular elaboration of eyes is quite out of

the question, nevertheless respond very definitely to the stimulation of light. They are said to be *positively phototropic* whenever they turn toward the source of light, as do the green leaves of a window plant, and *negatively phototropic*, when they turn away. Usually these responses are beneficial to the animal concerned, but not invariably so, for positively phototropic moths are known to commit suicide by flying into a flame.

Even as highly developed an animal as a vertebrate may possess photoreceptive integumental cells, located outside the eyes, since certain chameleon-like lizards, for instance, which normally respond to light by color changes in the skin, will make this response when temporarily blinded, if a stimulating ray of light, in an otherwise darkened room, is focused upon the skin.

B. Eyes

Eyes are the photoreceptive organs *par excellence*, and may be described as of two general sorts, namely, *direction eyes*, that distinguish light and dark, and enable an animal to locate the source from which the stimulus comes, and *image-forming eyes*, that report to the brain a more or less definite picture, reflected from objects in the environment.

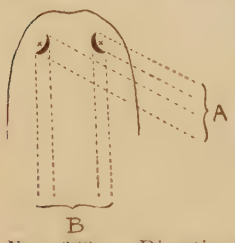


Fig. 663. — Direction eyes of a flatworm. *A*, diagonal direction of light; *B*, posterior direction of light; *x*, position of the photoreceptive cells within the crescentic pigment cup which acts as a shield.

1. Direction Eyes

Direction eyes are typically shown in flatworms (*Turbellaria*), which are found in the daytime out of reach of their enemies, clinging to the underside of stones and sticks submerged in shallow water.

The photoreceptive cells in direction eyes are packed closely together behind shieldlike cups of pigmented cells, through which the light does not penetrate (Fig. 663). The angles at which these cups are placed on the two sides of the head is such that it permits the light, whenever it does not fall exactly parallel to the long axis of the body, to stimulate the photoreceptors on one side more than those on the other side, so that the worm responds by turning until the stimulation received on both sides is equal. This results in *orientation* with reference to the source of light, and in a negatively phototactic flatworm, tends to carry it into darkness and safety.

2. Image-Forming Eyes

Image-forming eyes are optical devices that not only differentiate between the presence or absence of light, but also receive reflected light in such a way as to transfer a picture to the brain.

There are two outstanding types of image-forming eyes, namely, *mosaic*, and *camera eyes*. The former reaches its highest elaboration in the facetted eyes of insects, which far outnumber all other animals having eyes of any kind, but the latter is of greater present interest, because it is the type of the vertebrate eye.

a. MOSAIC EYES

Behind each facet of the compound eye of an insect, are several parts which together constitute an independent optical instrument for receiving light that has been reflected from external objects. This unit of the compound arthropod eye, is called an *ommatidium* (Fig. 664), and a cluster of these ommatidia together, sometimes several hundred in a single eye, produce a map of overlapping details that fit together, like the separate elements in a mosaic pattern, to form a single picture in the brain.

Usually the mosaic eyes of insects are set immovably in the head, but the convex exposure of their surfaces is such that the marginal ommatidia may point outward at angles sufficient to include in the whole eye a wide range of vision. In crustaceans it is usual for the mosaic eyes to be so mounted upon movable stalks that they may be turned in various directions, without the necessity of moving the rigid neckless head.

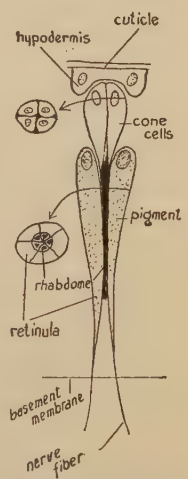


FIG. 664.—An ommatidium from the compound eye of a crustacean.

b. CAMERA EYES

A parallel between the typical camera eye of a vertebrate and a photographic camera, holds good for numerous details. Both are dark chambers with rigid walls, which admit the light through a focusing lens, guarded by a shutter-like arrangement that regulates the amount of entering light. Both have a sensitive receiving surface, lining that side of the chamber opposite the window where the light comes in, and in both there is an inversion upon the

sensitive screen of the image received. In one case the picture impressed upon the sensitive plate is "developed" after removal to an appropriate bath of chemicals. In the other instance, the picture received upon the sensitive retina of the eye, is transmitted by the optic nerve to the brain, which becomes the developer of it.

C. The Eyeball

The eyeball, or "camera box" of the vertebrate eye, is safely lodged in a bony orbit of the skull, forming a protection to it from mechanical injuries, except for a small necessary exposure on the

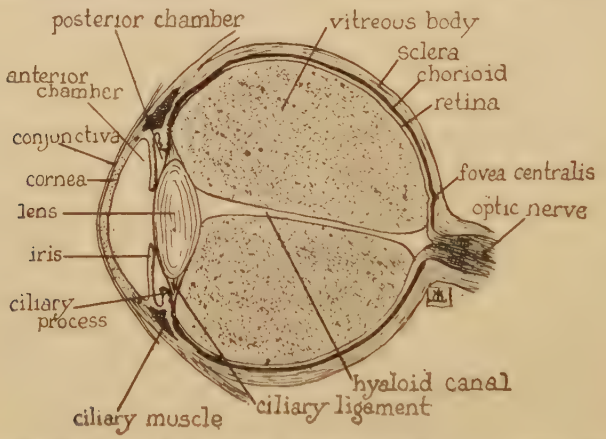


Fig. 665.—Diagram of a horizontal section through the human eye. (After Burton-Opitz.)

front face. It is held loosely in place by a fibrous membrane, called the *capsule of Tenon*.

The walls of the eyeball consist of three concentric layers of diverse tissues. The outer, or *corneo-scleral layer* is *skeletal* in function, maintaining the shape of the eyeball (Fig. 665). The pigmented middle, or *choroid layer*, which is primarily vascular in character, provides a place for nutritive blood vessels, while the inside *retinal layer* is sensory, and contains the "rods" and "cones," constituting the essential photoreceptive cells, to which all the other parts of the visual apparatus are subsidiary.

The large cavity within the inner retinal wall contains the *vitreous body*, a transparent, thick, semifluid mass, which helps to maintain the shape of the turgid eyeball.

There are two other cavities in the front part of the eye, the *anterior* and *posterior chambers*, filled with a watery lymph, which is being continuously renewed. These chambers are separated from each other by a diaphragm-like iris, and behind them is a dense, transparent lens that serves to focus the light so that it may fall sharply upon the sensory retinal expanse inside.

In addition to the eyeball itself, there are certain accessory structures, namely, muscles, glands, and the shutter-like eyelids, that are a part of the complex vertebrate eye.

D. The Human Eye

1. Its Structure

The outer skeletal layer of the human eye is made up of a tough, opaque, interwoven *sclerotic coat*, the "white of the eye," which occupies about five-sixths of the entire circumference, but is mostly out of sight within the orbit. The remaining one-sixth forms a transparent circular window, the *cornea*, over the front face of the eyeball, and is continuous with the white sclera. It is thinner in front (0.9mm.) than around the ring at the corneo-scleral margin (1.2mm.), where muscles that rotate the eyeball in the socket are attached.

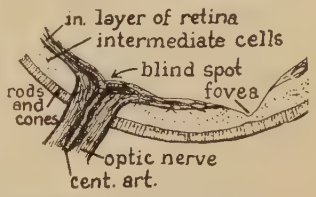


Fig. 666.—Diagram showing the entrance of the optic nerve into the eyeball. *Cent. art.*, central artery of retina. (After Bowditch.)

The outer skeletal layer is pierced by the optic nerve, and also by blood vessels.

The middle, or *vascular layer* of the wall of the eyeball, which is in intimate contact with the layers next to it, both inside and out, is made up of three regions, continuous with one another, namely, the chorioid, ciliary ring, and iris.

The *chorioid region*, characterized by an abundance of blood vessels, with the larger ones on the outside and a capillary plexus near the inner border, forms the larger part of this layer. The blood vessels supplying the eyeball (with the exception of the cornea), are the *central retinal artery* (Fig. 666), entering with the optic nerve and spreading out in the inner retinal layer; several (6–12) *short*, and two *long posterior ciliary arteries*, entering around the optic nerve and ramifying throughout the larger posterior part of the chorioid region; and four *anterior*

ciliary arteries, that form a plexus around the edge of the cornea (Fig. 667).

The returning blood vessels are several *anterior ciliary veins* from the anterior region of the eyeball, and four large *vorticose veins*, that pierce the walls of the eyeball in the equatorial region.

Communicating lymph spaces are also present in the eyeball, forming a ring, the *spaces of Fontana*, around the outer margin of the anterior chamber, and there is also a definite circular channel, the *sinus venosus sclera* or *canal of Schlemm*, which is in com-

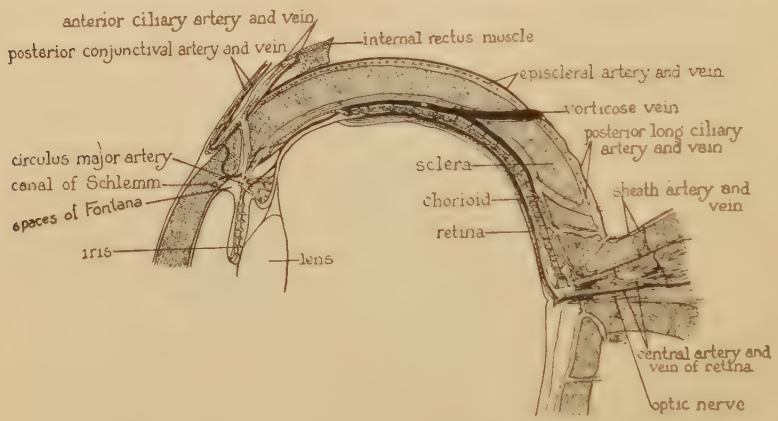


FIG. 667.—Blood vessels of the eyeball. (After Leber.)

munication with the spaces of Fontana, in the outer corneo-scleral layer, at about the region where the sclera passes over into the cornea.

Toward the front face of the eyeball the chorioid becomes thickened into a *ciliary ring*, which is extended into the disclike *iris*, with a round hole, the *pupil*, in the center of it. The pupil always appears black because it is an open window into a camera box in which no side lights can enter to be reflected out again.

The ciliary ring is made up of a foundation of fibrous connective tissue, the ciliary processes, and ciliary muscles. The *ciliary processes* are radiating ridges, sixty or seventy in number, extending centripetally, like inside cogs on a wheel, to the outer margin of the iris. They contain blood vessels, and furnish a point of attachment for the *suspensory ligament*, which stretches from them to the capsule surrounding the lens, serving to hold it in position.

The *ciliary muscles*, which have to do with properly changing the shape of the lens so as to focus the light sharply upon the retina, are smooth and involuntary in character, although their action is much more rapid than that of most involuntary muscles. They are arranged both radially and in circular fashion, with the latter muscles beneath.

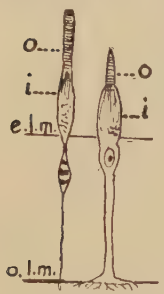


Fig. 668.—Diagram of a rod and of a cone. *o*, outer limb; *i*, inner limb; *e.l.m.*, external limiting membrane; *o.l.m.*, outer limiting membrane.

The *iris*, like the ciliary ring, is also supplied with both circular and radial muscles, that, by their contraction, either lessen or enlarge the size of the pupil, thus regulating the amount of light admitted to the eye, and, by acting as a diaphragm in front of the lens, preventing the occurrence of spherical and chromatic aberration.

Pigment of various kinds, which is characteristic of the vascular layer generally, is much more abundant in the iris, giving the distinctive color to the eye. Dilute black pigment, that makes "blue eyes," is universally located in the cells of the inner face of the iris of all human eyes except albinos. Whenever any other eye color is shown, as brown, gray, or black, it is due to the deposition of a pigment *dominant* over blue color, in the outer face of the iris.

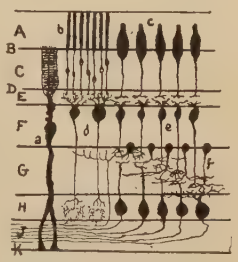


Fig. 669.—Diagram of retina. *A*, layer of rods and cones; *B*, *membrana limitans externa*; *C*, outer granular layer; *D*, Henle's fiber-layer; *E*, external molecular layer; *F*, inner granular layer; *G*, inner molecular layer; *H*, ganglionic cell layer; *J*, nerve-fiber layer; *K*, *membrana limitans interna*; *a*, Müller supporting cell; *b*, rods; *c*, cones; *d*, intermediate bipolar cells, connecting with rods; *e*, intermediate bipolar cells connecting with cones; *f*, amacrine cells. (After Cajal.)

The inner sensory, or *retinal layer* of the eyeball is a double, invaginated, gastrula-like cup, as its embryonic development shows, the outer part of which is a thinner stratum of pigmented cells, while the inner part is thicker, and made up of sensory photoreceptors, the *rods* and *cones* (Fig. 668), together with accessory cellular elements employed in their immediate service. Cone cells are probably chiefly useful in distinguishing color, while the rod cells perceive differences in light and dark, and detect objects in motion. Night animals, like owls and bats have fewer cones and more rods in the retina than do day animals.

A section through the inner layer of the retina shows a histological stratification into several component parts (Fig. 669). Next to the outer pigmented layer and interdigitating into it, are the projecting rods and cones. These form synapses with a stratum of *intermediate cells*, which in turn connect with a set of large *ganglionic cells*, whose neurites together form the optic nerve, extending outside of the eyeball to the brain. Thus, between the point of the reception of the stimulus and the brain, there are several chains, each made up of at least three sensory cells, (1) either a rod or a cone; (2) an intermediate cell; and (3) a ganglionic cell (Fig. 670). In the stratum of intermediate cells, there are also other cross-connecting elements, the *amacrine cells* (Fig. 669), which join together the triple systems laterally, as well as certain non-nervous *supporting cells*, extending from one face of the retinal layer to the other, and acting in a skeletal capacity.

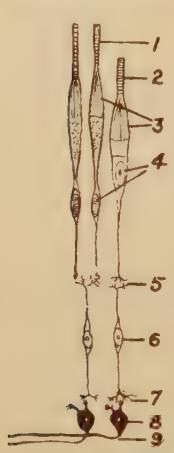


FIG. 670.—Diagram showing the three principal layers of the retina, with two rods and one cone in the outer layer. *1*, outer member of rods; *2*, outer member of cone; *3*, inner members of rods and cones; *4*, nuclei of rods and cones; *5*, synapse of rods and cones with bipolar intermediate cells; *6*, nucleus of intermediate cell; *7*, synapse with ganglionic cells; *8*, ganglionic cell bodies; *9*, fibers of ganglionic cells, which form the optic tract. (After Watson.)

The visual cells of the inner wall of the double retinal cup, do not extend all the way to the front face of the eye, but terminate in a somewhat irregular margin, the *ora serrata*, behind the ciliary ring.

The region of clearest vision in the retina is a small area in the line of the optical axis behind the lens and directly opposite the pupil (Fig. 665). This area, which is distinctly yellowish in color, is called the *macula lutea*. In its center is a conical depression, the *fovea centralis*, carpeted with more color-perceiving cones than rods and constituting the region of sharpest vision.

The optic nerve, which leaves the posterior part of the eyeball on the inner nasal side, forms a patch made up of the converging neurites of the ganglionic retinal cells, called the *blind spot*, because the photoreceptive rods and cones are absent there, and the rays of light striking it are consequently

not seen. The blind spot in the reader's eye may be easily demonstrated by reference to Fig. 671.

The lens is a cellular structure in which the component parts become transparent. It is compressible and elastic and is en-

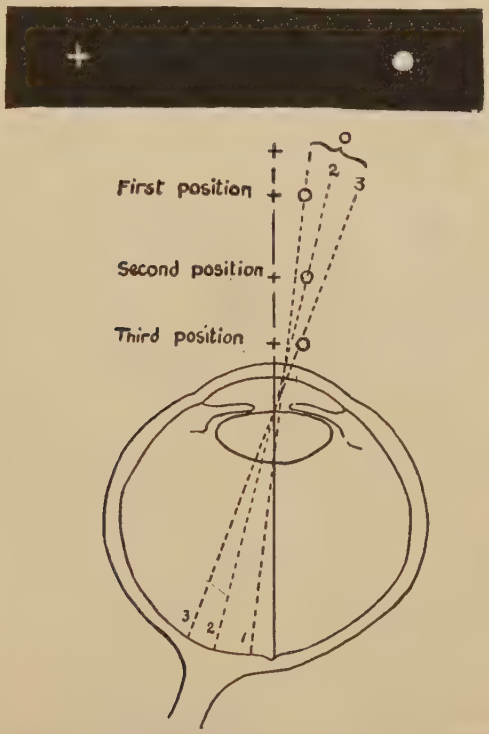


Fig. 671.—The blind spot of the eye. Hold the black figure straight in front of the eyes about a foot distant. Close the left eye and look at the white cross. You will see the round white spot also. This corresponds to the first position in the diagram. Now gradually move the page toward your eye. When you reach the second position the round spot will disappear, because the rays of light from it now fall upon the place where the optic nerve enters the eyeball and not upon the rods and cones of the retina. If the page is moved still nearer, the round spot will reappear, because light reflected from it now strikes the retina on the other side of the optic nerve, as shown by position 3.

closed within a thin capsule, continuous with the suspensory ligament which anchors it to the ciliary ring. The curvature of the posterior face is somewhat greater than that of the anterior face, and does not vary to any great extent, while the anterior curvature is readily modified by the tension which is

exerted on it through the ciliary muscles acting upon the enveloping capsule.

The lens rests upon a depression in the vitreous body, and anteriorly it is in contact with the pupillary margin of the iris. It serves to refract the rays of light that pass through it so that they will concentrate or focus upon the retina and produce a sharply defined figure.

2. Its Development

The retina is unique among sense organs in being originally a part of the brain. Early in development, before the medullary groove has closed into a tube, there are two lateral outpocketings in the diencephalic region of the brain. These hollow bulbous evaginations of the wall of the brain, the *optic vesicles*, push out laterally until they reach the enveloping ectoderm (Fig. 672). At points of contact the bulbs invaginate to form the double cups of the two-walled retina, later becoming enveloped from the surrounding mesodermal tissues by the vascular and supporting layers of the eyeball.

Fig. 672.—Outgrowth of optic vesicles and the formation of the lens in the chick. (After Duval.)

The cells of the inner retinal layer soon differentiate into rods and cones, intermediate, and amacrine cells, and large ganglionic cells, with their long neurites that together make the optic nerve. These neurites, which seem to penetrate the posterior wall of the eyeball, as a matter of fact grow out over the edge of the cup before a posterior wall is formed. As the primitive double cup invaginates, it has a notch in its brim, the *chorioid fissure* (Fig. 673), and through this gateway the

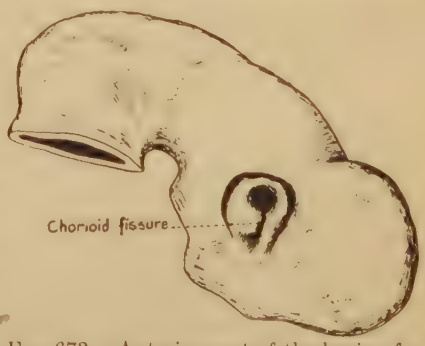


Fig. 673.—Anterior part of the brain of a human embryo of four weeks, showing chorioid fissure as a groove extending through the margin of the optic cup. (From Ziegler's wax-model, after His.)

sprouting neurites find egress, extending back to the brain along the *optic stalk*, like a vine upon a trellis. After the secondary connection of the optic nerve with the brain is complete, the optic stalk is absorbed, and the chorioid fissure closes by growth around the optic nerve, so that the latter has the familiar appearance of penetrating directly through the posterior wall of the eyeball.

Meanwhile, at the point of contact between the distal end of the optic stalk and the ectoderm, the lens is forming. This is brought about by the invagination of the ectoderm, which eventually pinches off a hollow capsule that becomes entirely disconnected with the outside ectoderm. The cavity within the embryonic capsule is gradually obliterated by the columnar growth of its posterior cells, which eventually fill the space entirely (Fig. 674), and become transparent.

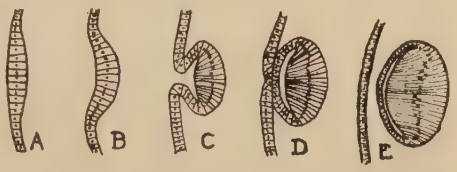


Fig. 674.—Development of the lens. (After Kingsley.)

3. The Inversion of the Retina

It will be observed that the rods and cones, unlike other sensory receptors, point *away* from the source of stimulation. The incident

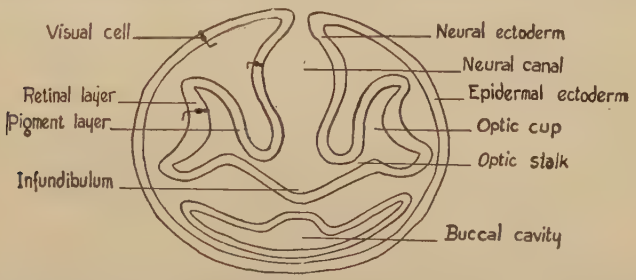


Fig. 675.—Diagram illustrating Balfour's theory to account for the inversion of the visual cells of the vertebrate retina. Transverse section through the head of a hypothetical vertebrate embryo, to show the morphological relations of the surfaces of the ectoderm of the integument, of the neural tube, and the forming retina. In each of these situations a single sense cell is indicated. (After Parker.)

light enters the eye through the cornea, lens, and vitreous body, and upon reaching the retina encounters the non-receptive ganglionic and intermediate cells before coming to the rods and cones, which, like a bashful child, have turned their backs upon the visitor.

This inconvenient and awkward inversion of the retinal sequence of cells finds an adequate explanation, as Balfour has shown, in the embryonic history of the retina. The ectodermal cells which become the rods and cones were originally arranged, like all other receptors, with their sensitive receptive ends facing the outside world from whence stimuli come, but, as the result of the invagination of the medullary tube, the evagination of the optic stalk and bulb, and the formation of the optic cup, they are finally left in the unfortunate position of inversion, as shown in Fig. 675.

Fig. 676. — Diagrams of the arrangement of pigment in the outer layer of the retina in a lizard's eye in darkness and after exposure to light. In light it is protectively diffused around the sensitive cones which project into the pigment layer. In darkness the pigment is withdrawn, thus exposing the cones. (After Luciani.)

The fovea centralis is the region of sharpest vision because at this point the intermediate and ganglionic cells are slanted or pushed over somewhat to one side out of the way, in an attempt to lessen the inaccessibility of the rods and cones to optical stimulation. Light entering the pupil of the eye at an angle instead of directly in the line of the optical axis, falls upon portions of the retina outside the fovea centralis (Fig. 666), and must, therefore filter through and between the intervening intermediate and ganglionic cells of the retina before it reaches the receptive rods and cones, that are even then hiding their sensitive ends between the pigmented cells of the outer retinal layer.

The amount of light reaching the rods and cones under all these difficulties is not only regulated by the iris, with its adjustable pupillary aperture, but also by the pigment in the outer retinal layer, which acts as a shield. This pigment shifts within the cells of the outer layer, by packing closely around the sensitive tips of the rods and cones when too much light impinges, or withdrawing to expose the tips, as occasion demands (Fig. 676).

4. Accessory Parts

The *extrinsic muscles*, which enable the eyeball to face in various directions without moving the entire head, have already been considered in another chapter (p. 574). They are inserted upon the eyeball far enough forward so that if contracted they do not

pull directly against their point of attachment, but against the curving surface of the eyeball, thus minimizing the danger of tearing loose (Fig. 677).

Eyelids are transverse protective folds of the skin that close like shutters over the front face of the eye. The inner surface of the lids, the *conjunctiva palpebrarum* (Fig. 678), is a reddish mucous tissue, continuous with the conjunctiva bulbi, that extends over the eyeball, making a thin transparent epidermis on the face of the cornea, through which light must pass on its way to the retina. The upper lid in man is larger and more movable than the lower and the aperture between the lids, or the *palpebral fissure*, is rather wider than in most mammals, showing some of the white sclera as well as the circular cornea. The edges of the palpebral fissure are supplied with a double row of *eyelashes*, larger above than below, which guard the sensitive conjunctival surfaces against dust particles and similar intrusions.

Fig. 677.—Diagram to show that the eyeball muscles are attached so far forward that they pull against the side of the eyeball, as indicated by the arrow, instead of directly at their point of insertion.

In the inner nasal angle of the eye there is present a vertical fold of the conjunctiva bulbi, called the *plica semilunaris*, that in many

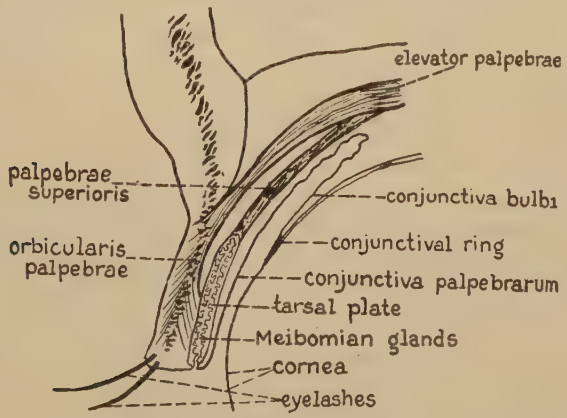


Fig. 678.—Vertical cut through the upper eyelid. (After Rouvière.)

vertebrates becomes extended into a movable third eyelid, or *nictitating membrane*, lying under the other two (Fig. 679).

Beneath the plica semilunaris is a small cavity, the *lacus lacri-*

malis, leading into the *nasolacrimal canal*, through which the excess of tears produced by the lacrimal gland, is ordinarily drained into the nasal cavity. The floor of the lacus lacrimalis is occupied by a small reddish elevation of the conjunctiva, the *caruncula lacrimalis*, which probably has to do with regulating the escape of tears through the nasolacrimal canal.

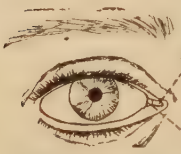


FIG. 679.—An eye showing the *plica semilunaris* and the *caruncula lacrimalis*. (After Wiedersheim.)

The eyelids are reinforced between the outer skin and the inner conjunctiva palpebrarum, by a stiffening fibro-muscular layer, the *tarsal plate*, containing numerous *Meibomian glands*, that pour out an oily secretion at the base of the eyelashes (Fig. 678).

The oily film produced by these glands serves constantly to seal the inner margin of the moving lids to the surface of the eyeball, and, when the eye is completely closed, to hold the margins of the two lids temporarily together. The lacrimal glands open by several short ducts inside the upper lid at the outer angle of the eye.

The occasional occurrence in man of lacrimal glands opening inside the lower lid (Fig. 680), is a reminder of the evolutionary journey they have made in order to arrive at their present position, for they have a similar position in amphibians and reptiles, with the lower lids more movable than the upper.

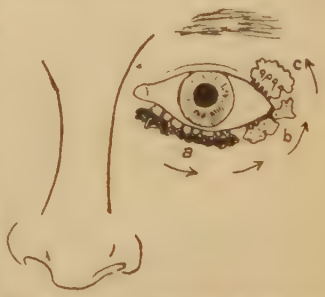


FIG. 680.—Diagram of the evolution of the lacrimal glands. *a*, position in amphibians; *b*, in reptiles and birds; *c*, in man. Sometimes in man the lacrimal glands are found located in the "*b*" position. (After Wiedersheim.)

Tears are a watery secretion from the lacrimal glands, and are continually produced, flowing in the form of a thin film over the exposed surface of the eyeball to drain eventually into the lacus lacrimalis and the nasolacrimal canal at the inner angle of the eye. They serve not only to keep the conjunctival and nasal membranes moist, but also to clean the surface of the eyeball of foreign particles that may accidentally find lodgment there.

Weeping, which is an overflow of tears, is peculiar to mankind, and is apparently a phyletically recent acquisition, connected with

certain emotional states that are not evolved in the lower animals. Consequently, as a comparative anatomist would expect, a human baby cannot *weep*, in spite of the presence of lacrimal glands, until it is about six weeks old, although it may demonstrate its ability to "cry."

E. The Median Eye

An ancestral median eye, either the parietal or the pineal body arising from the dorsal diencephalic region of the brain, is laid down embryonically in nearly all vertebrates. In certain cyclostomes both structures are represented as paired organs, with the parietal organ on the left and the pineal on the right side respectively, or more commonly, with the parietal organ crowded around into a position anterior to that of the pineal body.

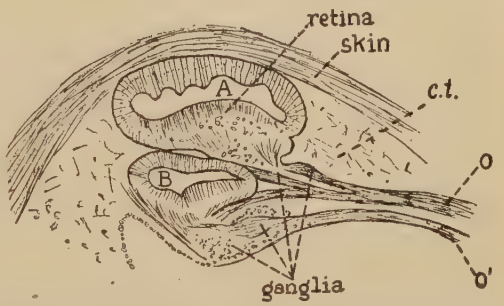


Fig. 681.—Median eye of *Petromyzon*. *c.t.*, connective tissue; *A*, and *B*, optic vesicles; *o.o'*, nerves. (After Owsjannikow.)

The *parietal organ* degenerates in the cyclostomes, most fishes, and amphibians, but develops into a true optical organ, with a retina and considerable structural complexity in certain lizards, particularly in *Sphenodon* (Fig. 681), the surviving representative from New Zealand of an otherwise extinct class of reptiles (Rhynchocephalia).

Only a trace of the parietal organ remains in birds, while in adult mammals it entirely disappears, and in many cases does not even put in a temporary embryonic appearance. In *Petromyzon*, the *pineal organ* assumes something of the character of an eye, and the same is true of the Anura, although in fishes generally it is relegated to the limbo of degenerate structures.

In mammals the pineal body has apparently entirely lost its original sensory character, and perhaps come to join the erratic fraternity of the endocrine glands.

The extinct *Stegocephali* had a conspicuous foramen through the top of the skull, like that in the skull of *Sphenodon* and certain modern lizards and anurans, which probably was for the accommodation of some sort of a median eye.

F. Comparative Anatomy

1. Amphioxus

Eyes are absent in amphioxus, but numerous photoreceptive cells are present, which are arranged along the nerve cord rendering these primitive vertebrates sensitive to light as it penetrates through the semi-transparent tissues of the body (Fig. 565). As would be expected, such cells point inward towards the cavity of the neural canal, since the inner walls of the latter, before invagination, were a part of the outside ectoderm which naturally faces towards the stimuli coming from the environment (Fig. 558).

2. Cyclostomes

The eyes of cyclostomes are degenerate rather than primitive. The eyeball is for the most part small and buried under a thick skin. It lacks cornea, iris, lens, and ciliary apparatus, although *Geotria macrophthalmus*, a fresh-water cyclostome from South America, is an exception, having unusually large eyes, as its name indicates.

There is no differentiation into rods and cones in the retina, for only elongated rods are present, indicating that rods, which are adapted to the reception of lights and shadows, and to the movements of external objects, rather than to the perception of colors, are phylogenetically older than cones.

3. Fishes

The *elasmobranch eye* is provided with a large rounded cornea, that aids the spherical lens in focusing, while the difficulty in seeing both forward and backward with eyes placed on the sides of a rigid neckless head, is partially compensated by the fact that the lens projects through the pupil against the cornea, so that "rays" of light coming at an extra wide angle are caught and concentrated upon the retina.

Eyelids, which are plainly simple folds of the skin, are present in many elasmobranchs, and the outer sclerotic layer is frequently reinforced by cartilage. The eyelids of the hammerhead shark, *Sphyrna*, are circular, which is perhaps the primitive form of eyelids. It is easy to see how the closure of eyelids of this type would be greatly facilitated by modification into upper and lower lids.

A *tapetum lucidum*, composed of some pigment and light-reflecting crystals, lines the inner surface of the chorioid layer

in many species. In some fishes there is a silvery or greenish-gold layer *outside* the chorioid, called the *argentea*, that likewise acts as a reflector.

The eyes of *teleosts* vary enormously in size, being large in pelagic carnivorous fishes, as well as in certain deep-sea fishes dwelling in regions of dim light, and small in bottom-feeders. The eyeball is usually much flattened on its front face, so that the optical axis is shorter than the axis through the equator. No eyelids, or glandular devices to keep the eyeball moist are present, but the unblinking eyes are in some measure shielded from the impact of water during locomotion by their lateral position.

Focusing is accomplished in the eyes of fishes, as in a camera, by *shifting the position of the lens* with reference to the sensitive retina, while in higher forms the same result is brought about by *changing the shape*, but not the position, of the elastic lens.

The eyes of fishes are normally nearsighted, that is, they are accommodated to near objects when at rest, so that focusing by shifting the position of the lens is called for only when more distant objects are brought into clear vision. In either case it is not easy to see at a distance through the denser light-absorbing medium of water. The opposite is true of the mammalian eye, which is normally farsighted. When at rest it is accommodated to distant objects, and a muscular exercise of the ciliary apparatus, which changes the shape of the stationary lens, is necessary in order to bring near objects into clear view.

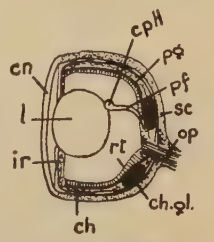


FIG. 682.—Diagrammatic vertical section through the eye of a teleost, *Salmo*. *ch*, chorioid; *ch.gl.*, chorioid gland; *cn*, cornea; *cpH*, *campanula Halleri*; *ir*, iris; *l*, lens; *op*, optic nerve; *pg*, pigment layer; *pf*, *processus falciformis*; *rt*, retina; *sc*, sclera. (After Parker and Haswell.)

The movement of the lens within the eye of a teleost fish, but not of an elasmobranch, is accomplished by means of a *processus falciformis*, a sickle-shaped organ containing blood vessels, nerves, and muscles, and having an enlarged end, the *campanula Halleri*, extending into the retinal cup through the chorioid fissure from the chorioid layer to the lens (Fig. 682).

There is apparently no focusing device in the eyes of elasmobranchs. According to Hess, fishes are practically color-blind,

for a histological examination of the retina reveals a great scarcity, or entire absence of color-perceiving cones. The fly fisherman therefore, who places his faith in the supposed allurement of highly colored flies, is not scientific in his procedure, that is, in the "exercise of common sense at its best." It is the movement and not the color of the fly, that makes it attractive to game fishes, and for this reason, it is highly improbable that the bright colors of tropical fishes have anything to do with the "sexual selection" of Darwin. They are more likely by-products of metabolic processes, that serve their possessors, if at all, as a useful camouflage against animals other than fishes, whose retinas are not so preponderantly made up of rods.

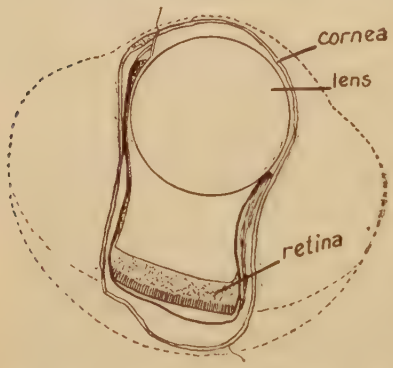


Fig. 683.—Median section through the telescopic eye of a deep-sea fish, *Agropelecus*, compared with the dotted outline of the normal eye of a fish. (After Franz.)

The fact that reflected light rays are bent at an angle when passing from air into the denser medium of water, makes it possible for a lurking fish sometimes to see, as if with a periscope, the approaching fisherman on the overhanging bank, before the fisherman can spy the fish.

Periophthalmus, the ambitious tropical climbing fish, that crawls out of water and lies in wait for flying insects upon the aërial roots of mangrove trees (Fig. 302), has so far improved upon the traditional fish eye as to anticipate the winking, disappearing eye of a frog, which may be depressed into a protective cavity in the skull, or popped out at will to view the surroundings.

Certain deep-sea fishes possess so-called *telescopic eyes*, with elongated eyeballs, enormous spherical lenses, and rounded corneas directed upward and pointing towards the source of sparse light above (Fig. 683).

4. Amphibians

In perennibranchiate amphibians, and aquatic urodeles generally, the eyes are small, without lids, and often sunken into the

skin. These animals apparently see with considerable difficulty, and then only near-by objects that are moving.

Even in the Anura, those amphibian aristocrats where lids and eye glands are present and adaptation to land life has been initiated, the eye is, in many particulars, simpler than that of fishes, for there is no tapetum or argentea associated with the chorioid, and the processus falciformis is wanting. The small lens, no longer spherical, is located entirely behind the iris, giving space for the anterior chamber of the eye, while the cornea is so rounded out as to have the effect of a second lens, making the animal shortsighted in the air when at rest, but farsighted when submerged under water, since the fluid in the anterior chamber has practically the same refractive index as that of the water outside, thus failing to focus the light as it passes through. As in fishes, the position instead of the shape of the rather inelastic lens is changed, in the process of focusing.

The nictitating membrane in the frog's eye, unlike that of higher vertebrates, is derived secondarily from the large lower lid, and is lubricated by the *Harderian glands*, which open into the conjunctival sac beneath it along the lower eyelid. Phylogenetically these are the earliest form of lacrimal glands.

The iris of the eye in many amphibians is brilliantly colored, being frequently golden, or shot with yellow flecks.

The pupil shows much variation in shape, being ordinarily round, but transversely oval in *Rana* and *Bufo*, vertically elliptical in *Alytes*, or even somewhat triangular in *Bombinator*.

The rods in the retina are considerably more numerous than the cones, and in the eye of *Necturus* they are the largest in size known for any vertebrate.

5. Reptiles

The eyes of reptiles are always decidedly lateral in position, so that they have little if any common field of vision. A lizard, for example, may spookily roll one eye upward, and the other backward or forward at the same time, thus seeing independently in two different directions at once. Focusing is effected by the improved method of changing the shape of the lens, rather than by shifting its position, as in aquatic vertebrates.

With the necessity for adaptation to land life, the reptilian eye is safeguarded against increasing dangers by means of well

developed eyelids and glands. In addition to the small upper, and the large and more movable lower lids, there is another transparent nictitating membrane, inside of the paired eyelids next to the eyeball.

Harderian glands supply this third eyelid along the ventral side, while true *lacrimal glands* put in an initial appearance in the region of the outer angle of the palpebral fissure. Both Harderian and lacrimal glands find an outlet for the excess of their secretions in the nasolacrimal canal. That the differentiation of tear glands is a comparatively recent acquisition among reptiles, is indicated by the fact that *Sphenodon*, that represents the most ancient of surviving reptilian types, is without tear glands.

Snakes, geckos, and certain limbless lizards living in intimate contact with the ground, are without movable eyelids, and their staring, unwinking eyes are protected by fixed, transparent, goggle-like windows of skin, shed in ecdysis, that are probably comparable with the nictitating membranes of other reptiles, since Harderian glands, which are the specific glands customarily supplying the nictitating membrane, are the only glands present.

The retina shows a considerable advance over that of amphibians in the relative number of cones as compared with rods, and in some reptiles there is even a suggestion of a depression into a fovea centralis, which is characteristic of higher mammals.

The iris of a reptile's eye is frequently highly colored, and in some turtles may even be of a different color in the male and female of the same species. The pupil is usually round, but it may be slitlike, either vertically or horizontally, particularly in snakes.

A ring of small supportive bones, the *sclerotic ring*, embedded in the sclerotic layer near the ciliary zone, was a characteristic feature of the ichthyosaurs and pterosaurs, long since extinct. Among modern reptiles it still survives, in less pronounced form, in many lizards and turtles.

6. *Birds*

There are certain species in every class of vertebrates *except birds*, which are either blind or possessed only of rudimentary eyes, but with these highly modified animals the sense of sight is absolutely indispensable in the struggle for existence. More-

over, no vertebrate eye excels that of birds, particularly birds of prey, in both complicated structure and efficient working, although accessory glands and muscles of the eyeball may be better developed in mammals.

The accommodation apparatus of the bird's eye is especially rapid and effective. Chickens, with their eyes focused closely upon the work of picking up small grains, become instantly aware of a predatory hawk, sailing like a vanishing speck high overhead, while the same hawk can drop with fatal precision upon a tiny mouse in a field, from a height that seems incredible to the possessor of human eyes.

The eye of birds, like that of many rapidly flying insects, is relatively very large, each one occupying fully as much space in the skull as the entire brain. If the human eye was proportionately as large as that of a bird, it would weigh, according to Tiedeman, as much as five pounds in a man weighing 175 pounds.

The eyeball of a bird is never spherical, but is constricted by a sclerotic ring in the ciliary zone, so as to produce a projecting and very conical corneal region, and a larger more flattened posterior part (Fig. 684). The retina contains more than one foveal depression of accentuated visibility, spreading out over a generous expanse that may extend as far as the equator of the eyeball. According to Slonaker, there is a preponderance of color-perceiving cones in the bird's retina.

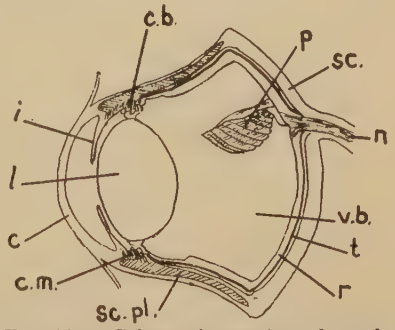


FIG. 684.—Schematic section through the eyeball of a bird, *Strix*. *c*, cornea; *c.b.*, ciliary body; *c.m.*, ciliary muscle; *i*, iris; *l*, lens; *n*, optic nerve; *p*, pecten; *r*, retina; *sc.*, sclera; *sc.pl.*, bony scleral plates; *t*, tapetum; *v.b.*, vitreous body. (After Haller.)

Projecting into the vitreous body of the bird's eye is an erectile fanlike organ of several folds, the *pecten*, which bears a superficial resemblance to the processus falciformis of the teleost eye, but probably is not homologous with it, since instead of entering the retinal cup through the chorioid fissure, it arises from the point of entrance of the optic nerve. The initial stages of the pecten are already seen in certain reptiles, and embryonic traces of it still persist in the mammalian eye (Fig. 685). Its function is not certainly

known but it seems probable that it regulates the pressure of fluids within the eye, and thus aids in the act of focusing.

The iris of the bird's eye contains striated muscle fibers, and is capable of more intensive contraction than is possible with the smooth muscles in the iris of the eyes of other vertebrates. The color of the iris varies considerably both with age and sex, and is characteristic for different species. In many parrots, for example, it is white, while in cormorants it is green; in swifts, blue; and in *Vireo olivaceus*, red. The whole expression of the otherwise immobile face of a bird, is centered in the lively iris. The pupil of a bird's eye is always round.

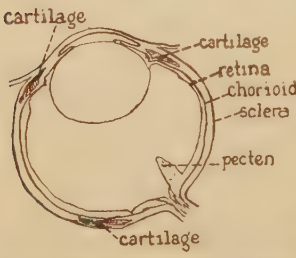


Fig. 685.—Diagrammatic horizontal section through the eye of *Chameleo*, showing rudiment of pecten, and sclerotic cartilages. (After Haller.)

The nictitating membrane is well developed, and is particularly useful to flying birds, being shut like transparent goggles over the face of the eyeball, and so preventing a flow of blurring tears during flight, which are normally called forth by the stimulating contact of the air against the rapidly moving cornea.

Harderian glands are usually large in the bird's eye, and the smaller lacrimal glands occupy the same position as in reptiles, at the outer angle of the palpebral fissure.

Owls have binocular vision, that is, they have both eyes trained upon the same field simultaneously, and in all birds the pointing of the eyes towards the source of optical stimulation, is greatly facilitated by the fact that the extremely mobile head is mounted upon a particularly flexible neck.

7. Mammals

The eye of mammals bears considerable resemblance to that of amphibians, in that typically the eyeball is nearly spherical. Smooth muscles are present in the iris, as well as in the ciliary apparatus, and the nictitating membrane is poorly developed.

The upper eyelids, unlike that of other vertebrates, are larger and more movable than the lower eyelids, while eyelashes with Meibomian glands are added. The eyelids of many mammals, such as mice, rabbits, and cats, are closed at birth, opening only after several days when the danger from wandering out of the nest is somewhat lessened.

There is no bony sclerotic ring, but a stiffening cartilage is present in the eyeball of the monotreme, *Echidna*. The sclera of whales is greatly thickened and resistent, possibly to withstand pressure from the surrounding water. The chorioid of the mammalian eye is very rich in blood vessels, whose turgor may in a measure compensate for the comparative lack of skeletal support in the walls of the eyeball.

In many mammals, particularly ungulates, carnivores, and cetaceans, there is a light-reflecting *tapetum lucidum* in the chorioid layer, but it is absent in man and the higher primates.

The superior oblique muscle of the eyeball is lengthened in man and made to pass through a tendinous pulley, whereby its efficiency is increased. The IVth cranial nerve (patheticus) which supplies this muscle has for this reason also received the name of *trochlearis*.

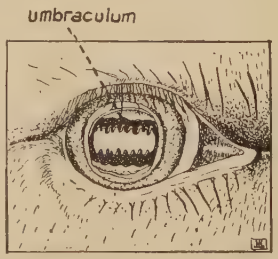


FIG. 686. — Umbraculum in the iris of a llama's eye. (After Plate.)

The tear glands for the most part move around to an externo-dorsal position, although Harderian glands along the region of the ventral eyelid are present in whales and such semiaquatic forms as the otter, hippopotamus, and seal.

The color of the iris varies among mammals generally, as it is well known to do in man. Thus, there are blue-eyed goats, yellow-eyed cats, and brown-eyed dogs. In certain ungulates, goats, camels, gazelles and coneys, the edge of the iris shows a peculiar modification, the *umbraculum* (Fig. 686), consisting of projecting granular bunches or flaps, which still permit some light to enter through small slits even when the iris is strongly contracted.

In many of the heavy-headed ungulates, the pupil is a transversely-oval aperture, that better enables the animal to sweep the horizon without swinging the head. In most cases, however, the pupil is round, although cats have a vertical slitlike opening in the iris, which in the seal is pear-shaped with the wide end next the nose.

The lens in the mammalian eye, particularly in man, is typically "lens-shaped." It is more spherical in water forms and is relatively largest in nocturnal and crepuscular mammals, such as bats, cats and mice. Nocturnal animals are further characterized by the absence or paucity of color-perceiving cones in the retina.

The ends of the rods in the mammalian eye are bathed by a chemical substance, *erythropsin*, or "visual purple," that acts as a sensibilator for increasing the receptivity of the rods to light. It is apparently secreted by the rods and not by the cones, as it is absent in such animals as snakes, turtles, poultry, and pigeons, in whose eyes scarcely any rods are present. It may become temporarily used up as the result of excessive or prolonged stimulation of light.

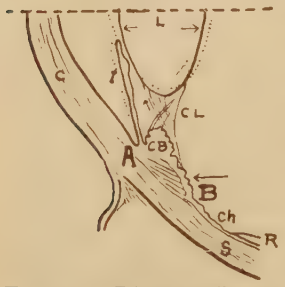


FIG. 687.—Diagram illustrating the process of accommodation in the human eye. *c*, cornea; *L*, lens; *I*, iris; *CL*, ciliary ligament; *CB*, ciliary body; *ch*, choroid; *R*, retina; *S*, sclera. In near vision the ciliary body contracts, drawing the region *B* nearer to the region *A*. The tension upon the ciliary ligament being diminished thereby, the lens assumes a more spherical shape, chiefly in the direction of the cornea. This change is indicated by dotted lines. (After Burton-Opitz.)

In the mammalian eye focusing is accomplished by contraction of the ciliary muscles, which releases the tension on the elastic lens, thus allowing it to assume a more spherical shape (Fig. 687). When at rest the mammalian eye is far-sighted, the lens being flattened by the compressing pull of the *fibers of Zinn* attached to its capsule. A muscular effort, therefore, on the part of the ciliary muscles, which pull against the taut fibers of Zinn, is necessary in order to lessen the confining pressure upon the elastic lens, and so to focus sharply upon the retina. This is the reverse of the operation of the ciliary apparatus in reptiles and birds, where, during accommodation, the focusing lens is subjected to increased compression, rather than relaxation.

Stereoscopic perception of distance, through triangulation resulting from binocular vision, is present in man and the higher primates, but most mammals, as well as the lower vertebrates, see two fields of vision simultaneously, instead of one.

It should be remembered that a little more than half the energy of extra-terrestrial light is appreciable to the photoreceptors of the human eye. About 43 per cent of the spectrum at the infra-red end, and 5 per cent at the ultra-violet end, is "out of sight." The 52 per cent remaining, that is, between ether wave lengths which at the violet end are 397 millionths of a millimeter in length, and at the red end 760 millionths of a millimeter, represents the entire

output of photic energy for which the human retina is adequate. Within these extremely minute limits lies the whole splendor and variety of our color world.

VI. INTERNAL SENSORY MECHANISMS

Most of the sense organs thus far considered belong to the category of exteroceptors, that is, sense organs adequate to receive stimuli arising outside of the organism. There are, however, sensations, resulting in part at least from stimuli originating within the animal body, whose receptors are little known, but which are nevertheless very real. No doubt many of the general sensations of the body, such as are described by the words *fatigue*, *nausea*, "feeling fit," or "run down," are without specific sense organs, being the result of the general tonus of several organs working together.

The problematical receptors that deal possibly with internal stimuli, have been divided into *proprioceptors*, "located in the deeper regions of the body, stimulated only indirectly by environmental forces, but excited by processes within the organism itself" (Mitchell), and *interoceptors*, "located in the linings of the digestive system, and stimulated by the conditions in this system."

1. Proprioceptors

These sense organs are closely related to pressure of some sort, acting (1) through muscles, tendons, and joints, as a "muscular sense," by means of which an idea of the weight of objects is gained, and the relative positions of the different parts of the body are realized; or (2) through internal organs, *nocireceptors*, that give rise to warning rheumatic or visceral pains; or (3) through the semicircular canal apparatus, already described in connection with the ear, to secure equilibration and orientation in space.

To gain a sensory idea of the weight of any object it is necessary to lift, or "heft" it, that is, to test by muscular resistance the pull of gravity which it exerts. For example, it takes twice as much muscular effort to keep a ten-pound ball from falling when it has been lifted into the air, as is necessary to sustain a five-pound ball in the same way, but this difference in the weight of the two balls is less accurately determined when they are simply placed successively upon the hand, without any muscular exertion, while it is resting upon a solid support.

The proprioceptive sense organs involved in the process of ascertaining the weight of objects, are located not only in the muscles, but also in tendons and joints, and they are quite distinct from cutaneous sense organs of pressure, that obviously supplement them in giving information about the character of ponderous objects.

2. Interoceptors

Appetite, hunger, and thirst are three distinct sensations, associated with the digestive apparatus, for which the adequate sense organs have not yet been discovered.

Appetite, that has been described as the "memory of food enjoyment," is brought about by internal changes in conjunction with external stimuli, such as the sight, odor, or taste of food. It is a pleasant sensation, not to be confused with hunger, which is an unpleasant sensation.

Hunger apparently has to do with muscular contraction of the walls of the empty stomach. It is an imperative safeguard against starvation, while the sensation of *thirst*, referred to the mucous lining of the throat, impels the animal to replace, if possible the loss of water from the body.

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